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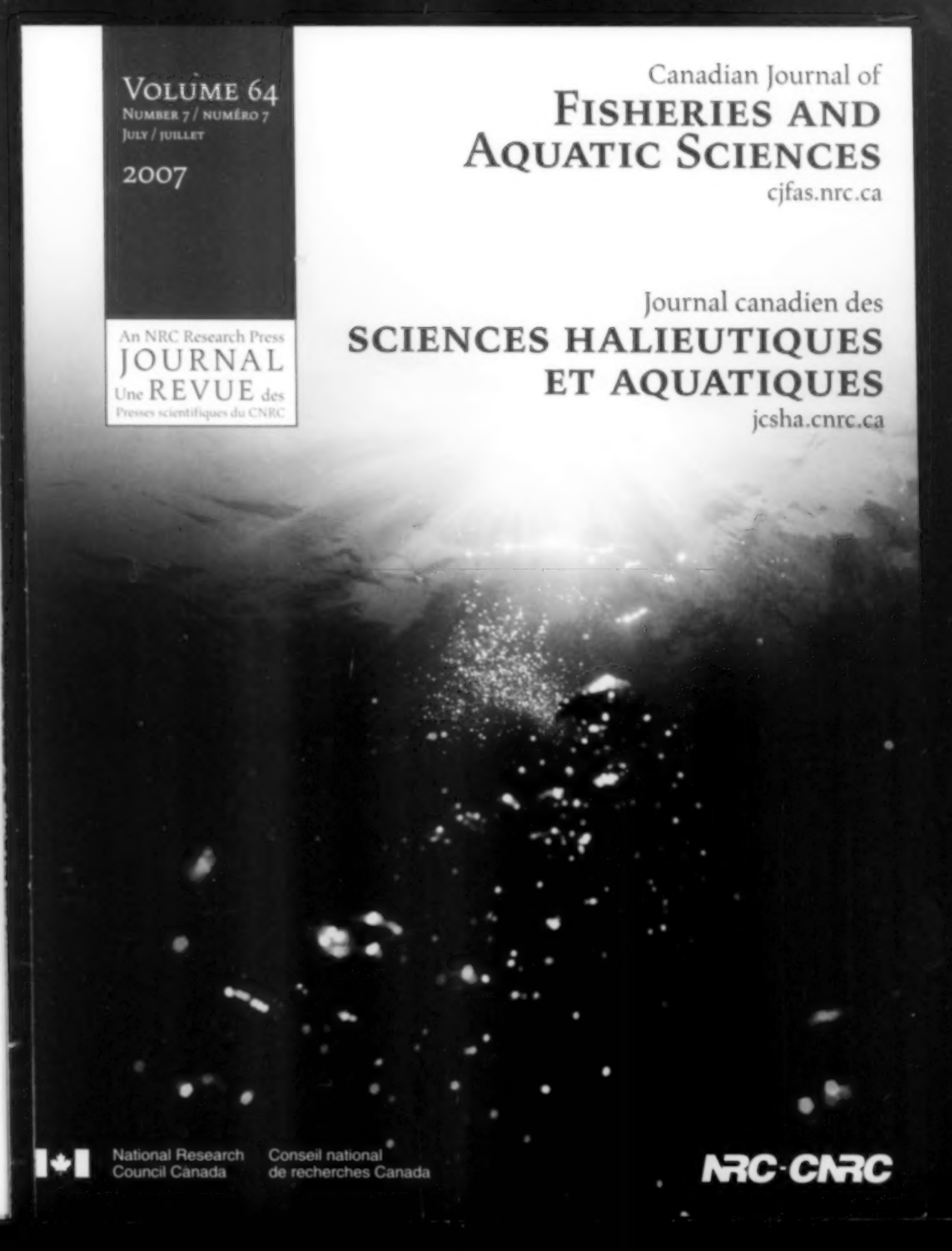

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Aggregated predators and vulnerability-independent mortality of prey

Thomas Torgersen

Abstract: I present a mechanistic predation model with explicit representation of predator aggregation for analysing the relationship between mortality rate of prey and their vulnerability (e.g., conspicuousness, escape ability). The model is developed for an aquatic setting with plankton as prey and planktivores as predators, but the principle is general. When predators are aggregated, encounters between prey and predators are not independent events. This means that a prey that runs into one predator is more likely to run into more predators, and any prey that runs into a high number of predators will eventually be perceived and captured, almost irrespective of how cryptic it is or how well it escapes attacks. A prey that has not run into a predator yet is more likely to continue to not run into predators and may therefore avoid predation even if it displays no crypsis or anti predation behaviour. Therefore, the predation risk from aggregated predators is less dependent on prey vulnerability than the intuitive proportionality relationship that applies to predation risk from solitary predators. This has important implications for patterns of mortality within prey communities (e.g., size dependency of plankton mortality).

Résumé : Le modèle mécaniste de prédation présenté ici comprend une représentation explicite de la contagion des prédateurs et sert à analyser la relation entre le taux de mortalité des proies et leur vulnérabilité (par ex., leur visibilité, leur capacité de fuite). Le modèle a été élaboré dans un contexte où le plancton sert de proies et les planctonophages de prédateurs, mais son principe est général. Lorsque la distribution des prédateurs est contagieuse, les rencontres entre les proies et les prédateurs ne sont pas des événements indépendants. Cela implique que lorsqu'une proie rencontre un prédateur, elle est plus susceptible d'en rencontrer d'autres et que toute proie qui vient en présence d'un grand nombre de prédateurs sera éventuellement repérée et capturée, presque sans égard à sa capacité de se camoufler ou d'échapper aux attaques. Une proie qui n'a pas encore rencontré un prédateur est plus susceptible de continuer à ne pas rencontrer de prédateurs et pourrait ainsi éviter la prédation, même si elle n'a pas de capacité de se dissimuler ou ne possède pas de comportement antiprédateur. En conséquence, le risque de prédation de la part de prédateurs à distribution contagieuse dépend moins de la vulnérabilité des proies que de la relation intuitive de proportionnalité qui s'applique au risque de prédation de la part de prédateurs solitaires. Ce phénomène a des conséquences importantes sur les patrons de mortalité dans les communautés de proies (par ex. sur la mortalité du plancton en fonction de la taille).

[Traduit par la Rédaction]

Introduction

Predation is a main source of mortality for most organisms. The ability and interest of a predator to detect and capture prey depends on prey characteristics, and predators therefore do not represent identical risks to different prey. Teasing apart the mechanistic relationships among environment, prey, and habitat characteristics and trophic interactions in real settings is a difficult task because of the level of complexity. In pelagic ecosystems, at least the physical complexity is generally low compared with terrestrial and benthic systems, with only a few continuous vertical gradients (light, temperature) and little physical horizontal structure. This has made it possible to formulate mechanistic models for pelagic predator–prey encounter and capture with realistic mathematical representation. Such models cover both perception of predators and prey through different sensory cues and escapement and capture probabilities (e.g., Eggers 1977; Aksnes and Giske 1993; Fiksen and MacKenzie 2002). Generally, larger prey are more easily detected by predators than smaller prey, but are also more able to escape attacks. Therefore, the predation rate by prey size curve is typically dome-shaped, both for predators on juvenile (Scharf et al. 1998) and larval (Bailey and Houde 1989; Paradis et al. 1996, 1999) fish, mesozooplankton (Pearre 1980; Greene 1986), and microzooplankton (Hansen et al. 1994). While small and young stages of fish larvae and mesozooplankton are preyed on by predominantly invertebrate predators, planktivorous fish are the dominating predators on larger forms. Planktivorous fish generally rely on vision for the perception of prey, and their search rate therefore decreases exponentially by depth (Aksnes et al. 2004). The size ratios between dominating planktivorous fish and their prey, including even large fish larvae and copepods, are generally >10. Accordingly, capture efficiencies of even small, postlarval planktivores (<10 cm body length) is typi-

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cally well above 0.25, even on large, negatively rheotactic prey (Drenner et al. 1978; Vinyard 1980; Utne-Palm 2000). Therefore, the clearance rate of planktivorous fish on mesozooplankton and fish larvae of different sizes is approximately proportional to visual search rate, which follows prey's visible area and visual contrast (Aksnes and Giske 1993; Aksnes and Utne 1997). Accordingly, larger fish larvae may experience much higher mortality rates than smaller ones (Pepin et al. 2002, 2003). Also, the deeper daytime distribution of larger zooplankton is generally understood as a response to intolerably high predation risk in shallow depths, while smaller forms suffer less risk at shallow depths (Zaret and Suffern 1976; Titelman and Fiksen 2004).

In animals, habitat choice and behaviour generally reflect compromises between growth and the risk of predation (Lima and Dill 1990); this is also true for small, planktonic organisms (Gliwicz 1986; Aksnes and Giske 1990; Titelman and Fiksen 2004). The relationships among predator, prey, and habitat characteristics and predation risk are instrumental in the understanding of mortality, and such understanding relies upon knowledge of both the spatial heterogeneity of predators and prey and on the mechanics of behavioural interactions between individuals. Even in a population of identical individuals, differing only in spatial position, probability of being eaten will vary because predators are not uniformly distributed. Luck will lead to some prey never encountering a predator, while others, if they live long enough, encounter several predators. If prey can perceive or foresee predator abundance, they can adapt to their local risk regime, considering both current risk and frequency and duration of high risk periods when deciding what to do (Lima and Bednekoff 1999). However, when predator abundance is not structured by physical habitat variables, prey must perceive predator abundance directly to respond to it, which may be difficult. Further, to reduce vulnerability when predator abundance is high, they must be able to respond adequately at a relevant time scale. Traits like size and morphology are very static and cannot be changed as a response to the perception of a sudden increase in predator abundance. On longer time scales (generations), entire clones or populations of plankton change body shape following the population dynamics of their predators (Dodson 1974), but this is not an option for a plankton individual upon the sudden discovery of an approaching predator group. To some extent, this reasoning is also valid for behavioural adaptations; if recent feeding history affects vulnerability (for instance through visibility of the gut of a planktonic copepod; Giguere and Northcote 1987; Tsuda et al. 1998), the increased vulnerability following the prey's actions cannot be reversed rapidly. Reduced vigilance may also affect the ability of prey to perceive increased predator abundance. Therefore, to a great extent, prey actions and traits must be chosen and evolve based on overall probabilities of experiencing different levels of predator abundances.

In ecological model studies, predator fields are usually represented as average abundances, and the spatial pattern and behaviour of predator distribution is not considered (Lima 2002). This is also the case for pelagic studies. Real predators are, however, often aggregated. This implies that an organism that runs into one predator is likely to run into more. Eggers (1976) showed how this leads to lower feeding rate of schooling planktivores compared with solitary ones. Implications of this for the prey may not be restricted to overall predation risk only (as a scaling factor), but may also be important for the qualitative risk regime (i.e., the relationship among environment and prey characteristics and mortality risk). In this paper, I address this question through a generic mathematical model and discuss the ability of prey to reduce their mortality risk through predation-evasive strategies. The analyses focuses on predation on zooplankton and fish larvae, but the principle is general.

Model description

All variables used below are listed at the end of this paper (see List of symbols). The relationship between a population's instantaneous mortality rate (m) and the individual survival probability per unit time of its members (p_{surv}) is as follows:

$$(1) \qquad p_{surv} = e^{-m}$$

When population sizes are large, p_{surv} also represent realised survivorship of the population. In a system where predators are randomly distributed and independently searching for prey, instantaneous mortality rate imposed on prey by predators is the product of predator density (N) and their individual feeding rate (I) divided by prey density (n):

$$(2) \qquad m = NIn^{-1}$$

An encounter-limited predator's feeding rate is proportional to prey density, leaving In^{-1} constant, while prey being hunted by handling-limited predators experience risk dilution at high prey densities. Here, I assume that predator feeding rate is limited by prey encounter rate and is therefore proportional to prey density. This assumption will generally be valid when predators have small perceptive range, when visual predators search in poor light conditions (e.g., at moderate or large depths or during dusk, night, and dawn), or when prey abundance is low. In situations when predators are handling-limited (e.g., large fish feeding on high densities of small prey in full daylight), the model presented here will not be valid. Predator search rate (V, space searched per time) is independent of prey and predator density. Applied to a pelagic setting, V is volume searched per time, but V could also be area searched per time. Capture efficiency (λ) is the probability that a prey within the perceptive range of a predator is killed. Thus,

$$(3) \qquad I = V\lambda n$$

and combining eqs. 2 and 3

$$(4) \qquad m = NV\lambda$$

Generally, λ and V depend on predator, prey, and environmental characteristics. I will refer to the product $V\lambda$ as the prey's vulnerability, following Greene (1986). For an individual prey to survive, it must successfully escape every time it encounters a predator. A prey that encounters X predators has the survival probability

$$(5) \qquad p_{surv,\,X} = (1 - \lambda)^X$$

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The expected predator encounter rate is $\hat{X} = NV$. When predators search independently of each other, predator encounters are Poisson-distributed. Mortality rate of a population in a spatial domain D can then be found through summing up the survival probabilities of all prey:

$$(6) \qquad m_D = -\ln \sum_{X=0}^{\infty} (1-\lambda)^X \frac{e^{-\hat{X}} \hat{X}^X}{X!} = NV\lambda < -\ln(1-\lambda)^{NV}$$

Thus, the simple relationship in eq. 4 results from the stochastic variability in how many predators each prey has to successfully escape from to survive. The overall mortality rate will always be lower than if all prey encountered the same number of predators. If predator abundance changes through time, the population's mortality rate within a time interval T_{int} equals the sum of mortality rates for all fractions of T_{int}:

$$(7) \qquad m_{T_{\text{int}}} = \sum_{T=1}^{T_{\text{int}}} m_T$$

Therefore, mortality rate is directly proportional to the average predator density during T_{int} ($N_{T_{\text{int}}}$) and insensitive to its temporal variability:

$$(8) \qquad m_{T_{\text{int}}} = N_{T_{\text{int}}} V\lambda$$

If, however, predator density varies in space, survival probability will differ between individuals. Let a spatial domain D contain S different habitats, differing in predator abundance and therefore in survival probability of prey per time (p_{surv_s}). A prey's probability of being in a given habitat is q_s. Assuming that initial prey densities are identical in all habitats, the surviving proportion of prey per time in this domain can be found from summing up the survival probabilities of all prey in the different habitats:

$$(9) \qquad p_{\text{surv}_D} = \sum_{s=1}^{S} p_{\text{surv}_s} q_s$$

and the population's mortality rate accordingly:

$$(10) \qquad m_D = -\ln \sum_{s=1}^{S} p_{\text{surv}_s} q_s = -\ln \sum_{s=1}^{S} e^{-N_s V\lambda} q_s$$

where N_s is the density of predators in s. The heterogeneous predator distribution causes higher mortality than average in some habitats and lower than average in others. The higher the density of predators, the more their search fields overlap. Therefore, survival probability decreases asymptotically towards zero with increasing local predator density, and because of this nonlinear relationship between instantaneous mortality rate and survival probability, increased survival in habitats with below average predator abundance more than outweighs the reduced survival in the high predator abundance habitats. Letting N_D be the average density of predators in D:

$$(11) \qquad m_D < N_D V\lambda$$

If aggregations or groups of predators move around within D, each location will experience temporal variability in predator abundance. This temporal variability reduces the differences in mortality between locations. However, when predators occur in aggregations or groups, prey that encounter one predator will, if they survive the first encounter, often encounter more predators from the same group. A group of predators can be considered a superpredator, and mortality rate imposed on prey by the predator groups can be found from the following equation:

$$(12) \qquad m_D = N_G V_G \lambda_G$$

where N_G is the density of predator groups, V_G is the search rate of the group (which is not related to the perception of individual prey by individual predators, but the rate with which a predator group occupies new space), and λ_G is the capture efficiency of the group (i.e., the proportion of prey within a space encountered by a predator group, which is ultimately captured during the predator group's retention time (t) within the space). The maximum value of λ_G is 1, so dense packing of predators in groups will reduce the group's search rate without a compensatory increase in its capture efficiency. This effect of overlapping search fields and therefore intragroup competition leads to lower overall mortality rate of prey when predators search in groups rather than as solitaires. At a given speed, a long (spatial extension in the moving direction) predator group will decimate the prey abundance within the encountered space for a longer time, and the relationship among t, group length (l), and speed (u) is

$$(13) \qquad t = lu^{-1}$$

Let the domain D be three-dimensional. I assume that predators have a cylindrical perceptive field with radius r. Their search rate is then

$$(14) \qquad V = u\pi r^2$$

assuming that search speed is identical with the group's net speed (u). If the movement trajectories and search paths of individual predators within the group are independent of each other, the number of predators each prey potentially encounters before the predator group leaves its location is Poisson-distributed. Letting N_g be the packing density of predators within the group, the capture efficiency of the group is

$$(15) \qquad \lambda_{G_{\text{indep}}} = 1 - e^{-lN_g \pi r^2 \lambda}$$

where the "indep" subscript means that predators within the group move independently of each other. Prey that encounter Y predator groups have the survival probability

$$(16) \qquad p_{\text{surv}_{Y_{\text{indep}}}} = e^{-lN_g \pi r^2 Y\lambda}$$

Assuming that the predator groups are cubic, their volume equals length cubed. The relationship among N_G, N_D, N_g, and l is

$$(17) \qquad N_G = \frac{N_D}{l^3 N_g}$$

The search rate of the group is the product of the front area of the group and its speed:

$$(18) \qquad V_G = ul^2$$

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Average number of encounters with predator groups per time ($\hat{Y}$) per prey is then

$$(19) \quad \hat{Y} = N_G V_G = \frac{N_D t}{N_g l}$$

If predator groups operate independently of each other, encounter rate with predator groups is Poisson-distributed around the average $\hat{Y}$:

$$(20) \quad m_{D_{indep}} = -\ln \sum_{Y=0}^{\infty} e^{-lN_g \pi r^2 \gamma \lambda} \frac{e^{-\hat{Y}} \hat{Y}^Y}{Y!} = N_G V_G \lambda_{G_{indep}}$$

If predators feed in an organised group that minimizes search overlap, like a polarized school of planktivorous fish, all prey encountering a predator group will encounter the search fields of (approximately) the same number of individual predators:

$$(21) \quad \lambda_{G_{dep}} = 1 - (1 - \lambda)^{lN_g \pi r^2}$$

where the "dep" subscript means that predators within the group move dependently of each other, so that all subvolumes are searched by (approximately) the same number of individual predators. Prey that encounter Y predator groups will then have the survival probability

$$(22) \quad p_{survY_{dep}} = (1 - \lambda)^{lN_g \pi r^2 Y}$$

Still assuming Poisson distribution of encounter rate with predator groups around the average $\hat{Y}$:

$$(23) \quad m_{D_{dep}} = -\ln \sum_{Y=0}^{\infty} (1 - \lambda)^{lN_g \pi r^2 Y} \frac{e^{-\hat{Y}} \hat{Y}^Y}{Y!} = N_G V_G \lambda_{G_{dep}}$$

For independently searching predators, r^2 and λ are factors in the same product, and the effect of a change in r^2 is identical with the effect of the same change in λ; this is not the case when predators search dependently of each other. However, the differences between vulnerability dependency of mortality imposed by groups where individual predators search independently of each other and not independently are small. In the following, I will only consider groups of independent predators.

Results

Predator aggregation pattern and prey mortality

When predators are locally abundant, they tend to have overlapping search paths (i.e., when a predator searches through a given space, it is likely that another predator has searched through it recently, and it is as likely that yet another will search through it soon). Therefore, when predators are aggregated, survivorship of prey can be more determined by spatial position than by vulnerability; most prey within a predator aggregation will be eaten, while those outside the aggregation will survive (Fig. 1). If predator distribution is aggregated and both predators and prey reside in the same patch over time (cf. eq. 10), the model predicts overall mortality of prey within the domain to be lower than if predators were evenly distributed, and the effect is more pronounced for vulnerable prey (Fig. 2*b*). The stronger the predator gradient, the smaller the difference in experienced mortality rate between prey with different vulnerabilities will be (Fig. 2*c*).

In the following, I have used parameter value ranges that are realistic for the interactions bewteen schooling, planktivorous fish and their prey. Overall predator abundance has been set to the high value of 0.1·m^{-3}, but this value acts as only a scaling factor and has no other effect on the results. Mortality rate of prey being hunted by solitary predators is determined by the search rate and capture efficiency of predators (Fig. 3*a*; cf. eq. 4). Mortality rate of prey being hunted by groups of predators (Figs. 3*b*–3*d*; cf. eq. 20) is also determined by the rate with which the group occupies new space. The model predicts that when predator groups are dense or large, individual predators will experience strong exploitative competition, reducing their feeding and predation rate. If predator groups have a given size (Fig. 3*b*), then $N_G \propto N_g^{-1}$, and λ_G increases asymptotically towards one with increasing N_g, resulting in a negative relationship between N_g and m. At a given packing density (Fig. 3*c*), $N_G \propto l^{-3}$. Since $V_G \propto l^2$, then $N_G V_G \propto l^{-1}$. The group's capture efficiency only increases asymptotically towards one with increasing l, causing a negative relationship between l and m. At a given density of predator groups (Fig. 3*d*), $N_g \propto l^{-3}$. Since $V_G \propto l^2$, then $m \propto l^1$ at lower values of l, when competition due to overlapping search fields is high ($\lambda_G \approx 1$). At high values of l, competition between individuals is weak ($\lambda_G \propto l^{-2}$), and m is independent of l.

The relationships between m and predator group parameters depend on the perceptive range of predators towards prey. The shorter the perceptive range of the predators, the weaker the competition and hence the relationship between school parameters and m (Fig. 4). Larger prey are visible at a longer range, and the maximum visual range for planktivores searching for small prey (mesozooplankton and fish larvae) is approximated by the following relationship:

$$(24) \quad r \propto b$$

where b is body length of the prey (cf. Aksnes and Giske 1993, and references therein). The lines representing different perceptive ranges (r) in Fig. 4 could therefore represent predators with different perceptive ranges, different light conditions (for a visual predator), or prey of different sizes, colour, or behaviour. In the case of different prey being visible at different ranges, it is clear from Fig. 4 that the mortality rate of highly visible prey is more influenced by predator group parameters than less visible prey. For prey that are invisible at ranges above 2 cm, mortality rate is almost the same at all group configurations, except when predators concentrate in a few extremely small and densely packed groups. Mortality rate of prey that are visible within 50 cm shows some dependency on group structure at all predator aggregation levels. Since r^2 and λ are factors in the same product in eq. 20, varying λ rather than r in Fig. 4 would produce the same patterns, meaning that mortality rate of prey that are good at escaping attacks is more influenced by predator group structure compared with the mortality rate of prey that are less able to escape. Perceptive range dependency and therefore size, colour, and behaviour dependency of mortality is reduced when predators search in groups (Fig. 5). This is most pronounced when groups are dense

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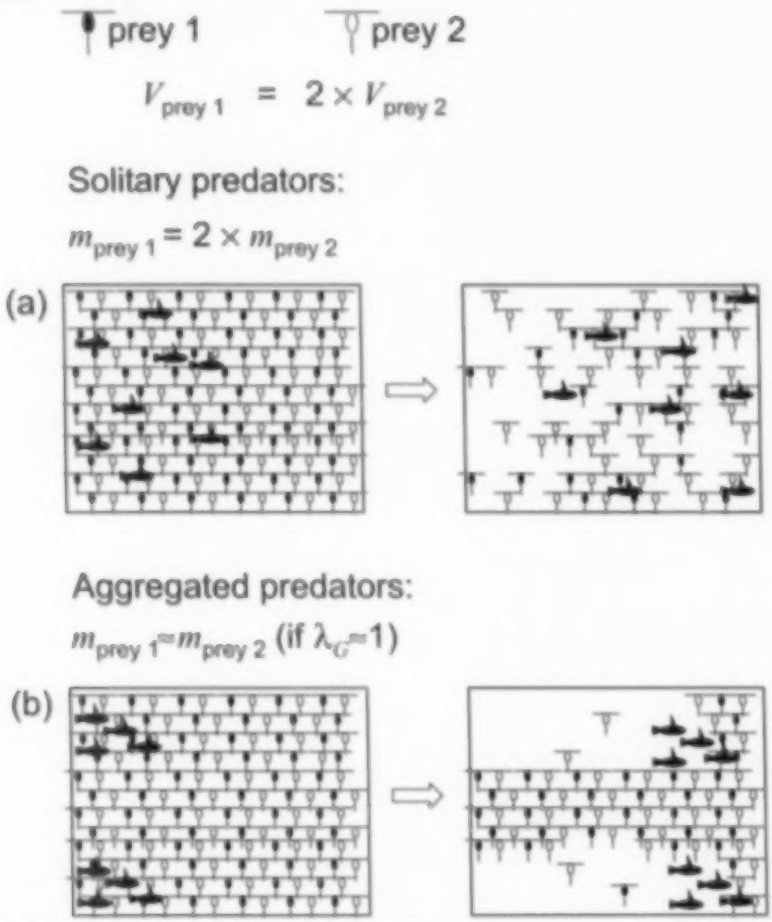
Fig. 1. Conceptual illustration of the predation of solitary and aggregated predators on prey differing in vulnerability. Predators have twice as high a search rate towards black prey as towards white prey. (*a*) When predators are solitary, the mortality rate they impose on prey is proportional to prey vulnerability. (*b*) When predators are aggregated in groups, overall mortality rates varies less between prey differing in vulnerability.



and rare (Fig. 5*a*; cf. Fig. 3*b*), large and rare (Fig. 5*b*; cf. Fig. 3*c*), and dense and small (Fig. 5*c*; cf. Fig. 3*d*). These situations correspond to high competition between predators and low overall prey mortality. Mortality rate as a function of λ rather than r would produce the same patterns as Fig. 5.

Aggregated predators and habitat use in the pelagic environment

Predator schooling has strong effect on depth (light)-dependent mortality. The maximum visual range (r) depends on light intensity and is here modelled according to Aksnes and Utne (1997), visual capacity parameter $E' = 3 \times 10^5$ and light half-saturation parameter $K_e = 5\ \mu E \cdot m^{-2} \cdot s^{-1}$ (for sunlight, 1 μE = 54 lx, giving $r = 27$ cm for a 2 mm prey at saturating light levels. Light decay is exponential through the water column, with a light extinction coefficient $k = 0.12\ m^{-1}$ and surface light = 300 μE. Predators are equally abundant at all depths. Solitary predators impose mortality on their prey proportional to b^2. In the upper ~20 m, predators experience light saturation, while below ~40 m, visual search rate is proportional to light (Fig. 6*a*). Mortality imposed on prey by schooling predators is less dependent on prey size at shallow depths, since λ_G then is high even for small prey. Large prey experience approximately the same mortality down to rather large depths (~60 m for 4 mm prey), since λ_G is high even at low light intensities for large prey (Fig. 6*a*). Size dependency of mortality increases with depth when predators school, and the relative survival of small prey compared with large prey at different depths depends on the school parameters (Fig. 6*b*). Small prey experience relatively higher mortality when predators form few and dense (Fig. 6*b*, left panel) or few and large (Fig. 6*b*, center panel) schools or when schools containing a given number of individuals have high packing density and small size (Fig. 6*b*, right panel).

Varying abundance of aggregated predators and prey mortality

If average predator abundance increases, the effect on mortality of prey is determined by whether the predators form more, larger, or denser groups (Fig. 7). If the increase in predator abundance results in denser or larger, rather than more pred-

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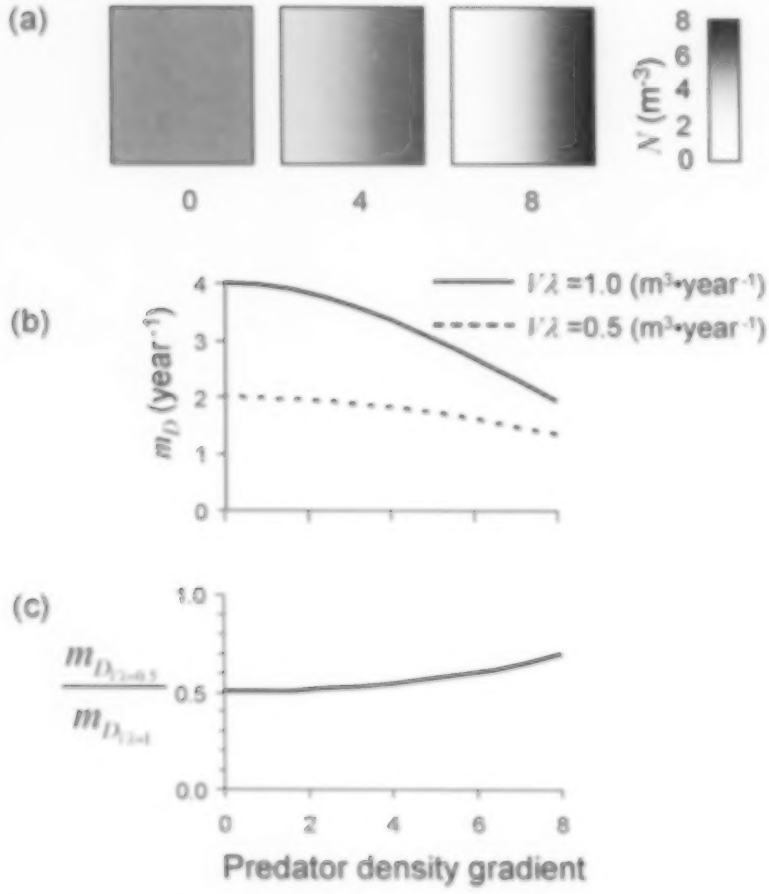
Fig. 2. Instantaneous mortality rate of prey as a function of static predator abundance gradients, following eq. 10. Prey are assumed to be equally abundant within the entire domain initially and to not move within it. (*a*) The domain is divided into 21 habitats, and predator density increases linearly from left to right within the domain. When predator density gradient is 0 (left panel), all habitats have a predator density of 4·m^{-3}; when it is 4 (centre panel), predator density increases from 2 to 6·m^{-3} (from left to right), and when it is 8, it increases from 0 to 8·m^{-3}. (*b*) Mortality rate of the prey population within the domain for $V\lambda$ = 0.5 m^3·year^{-1} (low vulnerability) and $V\lambda$ = 1 m^3·year^{-1} (high vulnerability) at different predator density gradients. (*c*) Ratio of mortality rate of prey with low vulnerability to mortality rate of prey with high vulnerability.



ator groups, it will result in a larger overlap in search fields. Following eq. 12, if varying predator abundance results in varying number of predator groups ($N_G \propto N_D$), mortality rate is always proportional to overall predator abundance (Fig. 7*b*), as is the case for solitary predators (Fig. 7*a*). This means that the ratio of mortality rate of prey with high vulnerability (r or λ) to that of prey with low vulnerability will be independent of predator abundance. If varying predator abundance results in variable size of predator groups ($l^3 \propto N_D$), the relationship between overall mortality rate and predator abundance is not linear: $V_G \propto l^2$ at all ranges of l, while λ_G increases asymptotically towards 1 with increasing l (eq. 15), so that $\lambda_G \propto l$ at very low values of l, and $\lambda_G \propto l^0$ at very high values of l. Therefore, if $l^3 \propto N_D$, then $m_D \propto N_D$ at very low values of l and $m_D \propto N_D^{2/3}$ at very high values of l. Mortality rate of vulnerable prey will level off at lower predator abundances than the mortality rate of less vulnerable prey, and the ratio of mortality rate of prey with high vulnerability to that of prey with low vulnerability will decrease with increasing predator abundance (Fig. 7*c*). If varying predator abundance results in varying packing density of predators within groups ($N_g \propto N_D$), an increase in overall predator abundance will only cause a substantial increase in m_D at low packing densities, especially for vulnerable prey (Fig. 7*d*): $V_G \propto N_g^0$, and $\lambda_G \propto N_g^3$ at very low values of N_g and $\lambda_G \propto N_g^0$ at very high values of N_g. Therefore, if $N_g \propto N_D$, then $m_D \propto N_D$ at very low values of N_D and $m_D \propto N_D^0$ at very high values of N_D. In this situation, mortality rates of prey with different vulnerabilities will all approach the asymptote $N_G V_G$ as predator abundance increases.

Discussion

It is a well-established fact that abundant predators reduce the abundance of their food resource, thereby competing with each other exploitatively. More specifically, the negative relationship between planktivorous feeding rate and schooling is also established (e.g., Eggers 1976; Freon and Misund 1999). From the prey's point of view, this means

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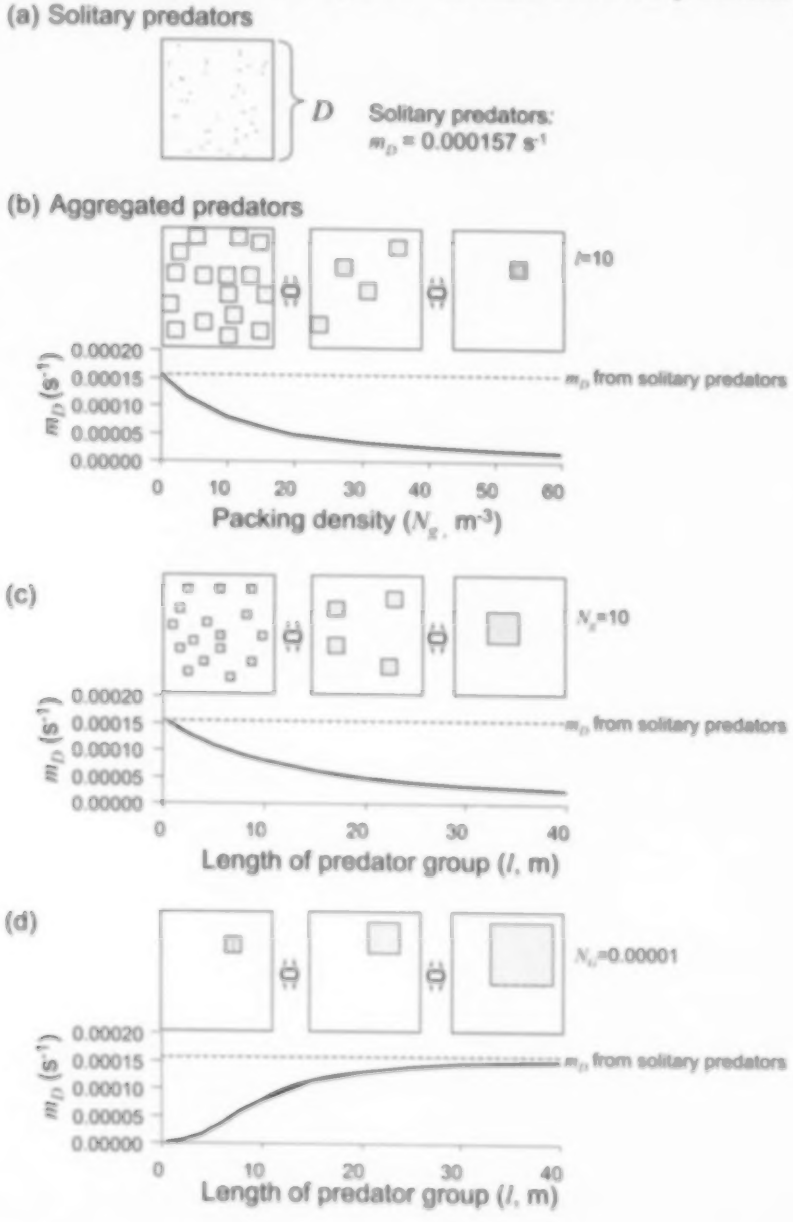
Fig. 3. The relationship between prey mortality rate and predator aggregation. As in Fig. 2, prey are assumed to be equally abundant within the entire domain initially and to not move within it. As opposed to Fig. 2, predator groups move within the domain: N_D = 0.1·m^{-3}, λ = 0.5, u = 0.1 m·s^{-1}, and r = 0.1 m. (*a*) Solitary, independent predators, following eq. 4. (*b*–*c*) Predators searching in groups, following eq. 20. Broken lines represent mortality imposed by solitary predators. (*b*) Spatial extension of groups is constant, and predators form many dilute or few dense groups. (*c*) Predator density within groups is constant, and predators form many small or few large groups. (*d*) The number of groups is constant, and predators form small and dense or large and dilute groups.



that aggregated predators impose less risk. Here, I have presented a model that predicts that when this is the case (i.e., when predators in an aggregation substantially diminish the food resources it encounters), the relationship between prey vulnerability and mortality is decoupled. This is because the perceptive range and capture efficiency has a larger influence on where in the school a prey will be eaten than on whether it will be eaten, and in the most extreme case, encountering a group of predators is equivalent to death independently of vulnerability. Further, when pelagic prey are being hunted by schooling or aggregated visual predators, prey with low vulnerability experience a larger increase in survival by descending to darker depths than more vulnerable prey do. The reason for this is that the survival probabil-

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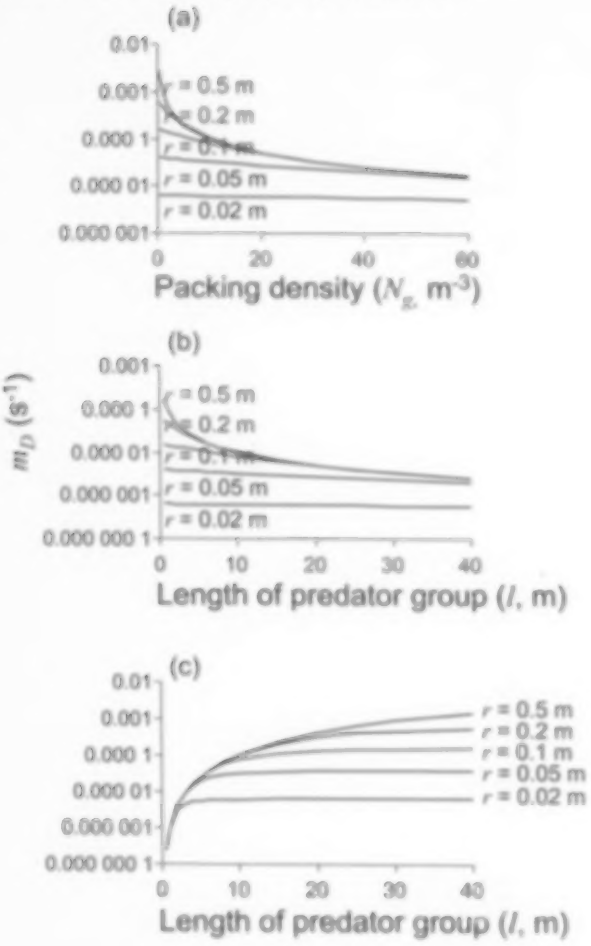
Fig. 4. Mortality rate by group structure at different search ranges. The panels follow Figs. 3*b*–3*d*. Predators within groups search independently of each other: $N_D = 0.1 \cdot m^{-3}$, $\lambda = 0.5$, and $u = 0.1\ m \cdot s^{-1}$. (*a*) Spatial extension of groups is constant, and predators form many dilute or few dense groups; $l = 10$ m. (*b*) Predator density within groups is constant, and predators form many small or few large groups; $N_g = 10 \cdot m^{-3}$. (*c*) The number of groups is constant, and predators form small and dense or large and dilute groups; $N_G = 0.00001 \cdot m^{-3}$.



ity of inherently vulnerable prey that encounter a predator school is close to zero even at rather low light levels, while less inherently vulnerable prey can have a considerable survival probability at darker depths, even if it encounters a predator school.

Occurrence of vulnerability-independent mortality in nature

The importance of the predicted relationships from the presented model in nature is potentially substantial, since all organisms are heterogeneously distributed on some scale. About 80% of the world's fish species school at some stage in their lives (Burgess and Shaw 1979), and in particular, important epipelagic, planktivorous fishes like herring, anchovy, and mackerel species are obligate schoolers as juveniles and adults. Also, many important invertebrate planktivores are known to form schools or other types of dense aggregations, including squids and krill (reviewed by Ritz 1994). The exposure to migrating, social predators is not unique to plankton and is equally relevant to all potential prey in different systems. What is special for plankton is that they are less able to distribute actively relative to topography and geography than their predators. Therefore, advection transports plankton across, between, or outside resident aggregations of planktivores, and the patterns of imposed mortality on plankton by such aggregations should be the same as those of moving schools. Advection within coastal areas may lead to substantial consumption of plankton by littoral planktivores (Salvanes et al. 1992). Perhaps more importantly, planktivores are often associated with shelf breaks and other topographical features (Wolanski and Hamner 1988). This applies to schools of epipelagic fish (reviewed by Freon and Misund 1999), nonschooling mesopelagic fish and macroplankton (Reid et al. 1991; Torgersen et al. 1997; Genin 2004), and demersal planktivores (Isaacs and Schwartzlose 1965; Genin et al. 1994).

Having established that planktivores often are aggregated, the effect of these aggregative patterns in decoupling the relationship between vulnerability and mortality of prey relies on the planktivore aggregations' ability to considerably reduce the density of plankton prey upon encounter. Such evidence exists for different types of aggregations on different scales; Koslow (1981) estimated the proportions of differently sized prey consumed by comparing plankton samples taken inside and outside the wakes of northern anchovy (*Engraulis mordax*) schools. More than 50% of the individuals of most size groups of prey were eaten. Further, there was little or no difference in the size of the remaining fractions between the larger prey groups, and this observation is in accordance with the patterns predicted by the model. Apparently, the schooling behaviour of the anchovies reduced size dependency in the mortality rates of plankton by eating almost all prey within a wide size range, but of course only within the encountered volume. Paradis and Pepin (2001) suggested that "Future studies should investigate how a nonrandom spatial distribution of pelagic fishes affects the characteristics of surviving larvae", and later, Pepin et al. (2003) did not find the expected increase in predation rates with size in larval radiated shanny (*Ulvaria subbifurcata*) subject to predation from their schooling predator capelin (*Mallotus villosus*). Such a finding is also in accordance with the model predictions presented here. Intense grazing of planktonic prey in the vicinity of topographical features (summits, seamounts, coral reefs) resulting in large local reductions in plankton abundance has also been reported with compelling evidence (e.g., Genin et al. 1994; Haury et al. 1995, 2000). The ability of such topographically controlled aggregations of planktivores to daily generate meso-scale patchiness suggests that mortality rates experienced by plankton in areas where topography shapes planktivore distributions may have less relationship with their vulnerability and more with advection and topography. In large, advective systems, individual plankton may spend their entire life within an area with high or low predator abundance, but with little or no intergenerational retention within each such area. I will use

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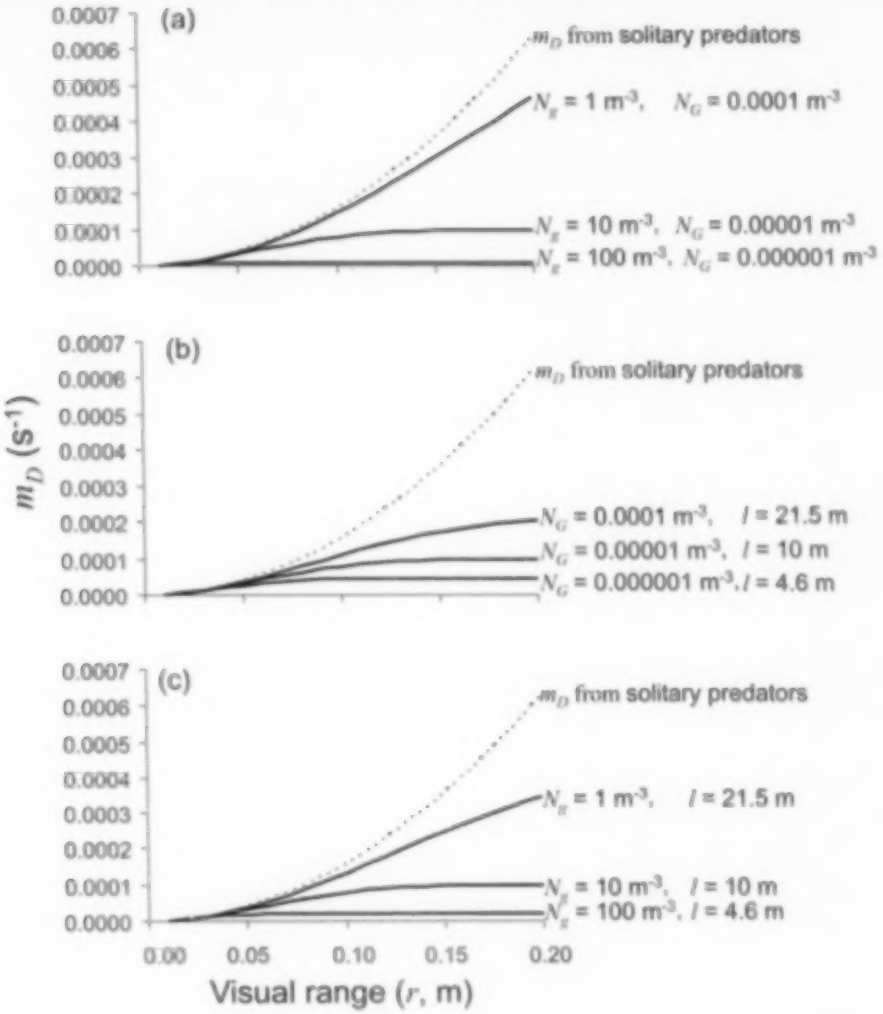
Fig. 5. Mortality rate by search range at different group structures. Predators within groups search independently of each other: N_D = 0.1·m^{-3}, λ = 0.5, and u = 0.1 m·s^{-1}. (*a*) l = 10 m; (*b*) N_g = 10·m^{-3}; (*c*) N_G = 0.00001·m^{-3}.



the large calanoid copepod *Calanus finmarchicus* in the Nordic Seas as an example of this. Large populations of Atlantic mackerel (*Scomber scombrus*) and Norwegian spring-spawning Atlantic herring (*Clupea harengus*) spend months of the summer season in the Nordic Seas, occupying large parts of the ocean, while other parts are outside the range affected by the feeding migrations of these important planktivores (Misund et al. 1998; Kaartvedt 2000). Their main prey is *C. finmarchicus*, and their estimated annual consumption of this population is of the same magnitude as its estimated annual production (Kaartvedt 2000; Dommasnes et al. 2004; Varpe et al. 2005). This consumption must be restricted to the areas that are in fact visited by the planktivores, and the *C. finmarchicus* individuals that survive spring–summer in this advective environment may generally be those outside the feeding areas of these predators; vulnerability may have little influence on survival. *Calanus finmarchicus* descends to mesopelagic depths for overwintering during summer, thereby partly avoiding their migrating epipelagic predators (Kaartvedt 2000). There is extensive large-scale variability in density of mesopelagic planktivores in the Nordic Seas (Torgersen et al. 1997; Dalpadado et al. 1998; Dale et al. 1999), and fjord studies have shown that mortality during winter is determined by density and composition of mesopelagic macroplankton and micronekton (Bagøien et al. 2000, 2001). Hence, the relationship among mortality, developmental stage, and behaviour of *C. finmarchicus* should be substantially modulated towards less vulnerability dependency by the heterogeneous, large-scale distribution of their predators during both the growth season and overwintering.

Implications for adaptive strategies

Survival and growth are generally conflicting demands, and fitness is maximized at some optimal trade-off function between the two (Lima and Dill 1990; Houston et al. 1993).

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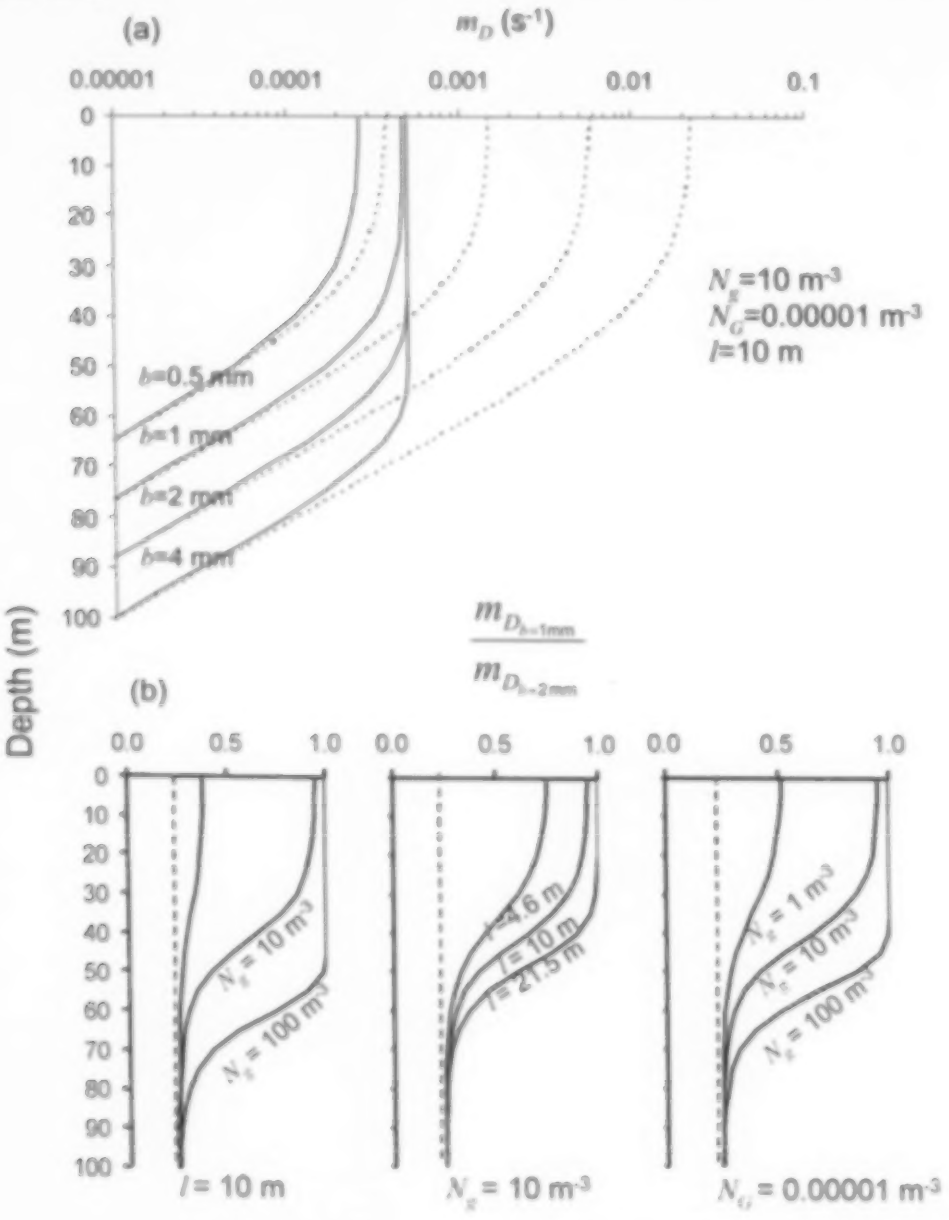
Fig. 6. Predators within groups search independently of each other: $N_D = 0.1 \cdot m^{-3}$, $\lambda = 0.5$, and $\alpha = 0.1$ m·s^{-1}. (*a*) Mortality rate by depth for prey of different sizes being hunted by schooling (solid lines) and solitary predators (broken lines). (*b*) The ratio of mortality rate of a 1 mm prey to that of a 2 mm prey by depth for different predator group characteristics. The vertical line shows the ratio when predators are solitary.



In most model studies addressing this trade-off in plankton, mortality is assumed to be proportional to prey vulnerability and predator density, both when vulnerability varies with prey and habitat traits (Hugie and Dill 1994; De Robertis 2002; Titelman and Fiksen 2004). However, if predators are aggregated, the mortality reduction obtained from a reduction in growth is smaller than the obtained vulnerability reduction. Therefore, such models will consistently bias the growth–survival trade-off towards more survival-focused strategies. A general finding from this model is that being (*i*) difficult to perceive, (*ii*) good at escaping, or (*iii*) unattractive to eat are less efficient predation-evasive strategies when predators are aggregated. The more aggregated the distribution of predators is, the less sensitive to risk should fish larvae and zooplankton be. Contrary to intuition, the least vulnerable prey have the most to gain from predation-

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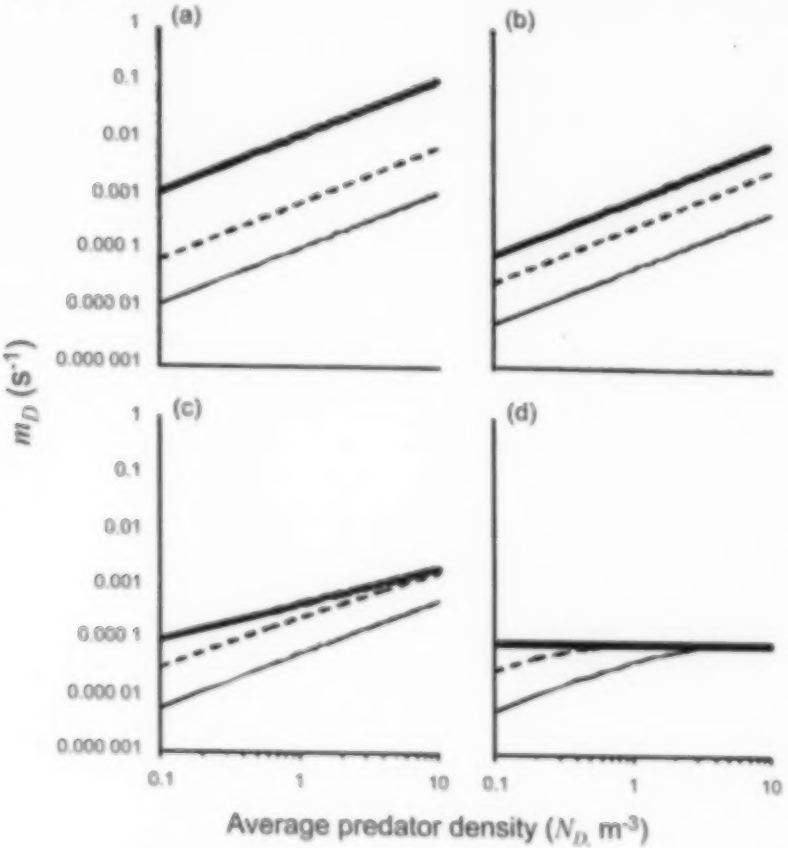
Fig. 7. Mortality rate of prey by average predator abundance for three values of search range (r): r = 0.20 m (thick line), r = 0.05 m (broken line), r = 0.02 m (thin line). Predators within groups search independently of each other: λ = 0.5 and u = 0.1 m·s^{-1}. Panel *a* shows mortality rates imposed by solitary predators. Panels *b*–*d* show mortality rates imposed by predator groups when a change in predator abundance occurs as a change in (*b*) number of predator groups (N_G increases, 0.00001–0.001·m^{-3}), (*c*) group size (l increases, 10–46.4 m), or (*d*) packing density (N_g increases, 10–1000·m^{-3}). Group parameter values at N_D = 0.1·m^{-3} for panels *a*–*c*: N_g = 10·m^{-3}, N_G = 0.00001·m^{-3}, l = 10 m.



evasive strategies when faced with aggregated predators. This is because at any given pattern of predator aggregation, there is a stronger relationship between the group's capture efficiency and prey vulnerability for inherently invulnerable prey. Predator-evasive strategies that reduce spatial overlap with predators are, however, equally effective when predators are aggregated as when they are not — provided that the lower predator abundance corresponds to lower density of groups and not to smaller packing density within groups. However, since predators are able to follow prey (cf. Giske et al. 1998) and schooling predators are less dependent on prey detection distance (Fig. 5*a*), reducing spatial overlap with predators may be less of an option. A prediction from this model study is that when predators are aggregated, adaptive trade-off models assuming random predator distribution should predict more conspicuousness-reducing traits than those observed, but discrepancies between observations and predictions should be less pronounced when it comes to predator-evasive strategies like refuge use and timing of hibernation.

Dynamic aggregations

Predator aggregations are variable, and to use this model approach to say something quantitative about the relationship between prey characteristics and mortality in real systems, time budgets for predator spatial structure is required. Mesopelagic macroplankton and mikronekton are usually found in rather dilute scattering layers, but there is considerable patchiness within such layers (Torgersen et al. 1997; Benoit-Bird and Au 2003), and they sometimes form very dense schools (Kaartvedt et al. 1998, 2005). The schooling dynamics of epipelagic, planktivorous fish have been found to be highly variable and dynamic, and within the same population, swimming speed, school size, and packing density varies with orders of magnitude (Misund et al. 1995; Godo et al. 2004). This does not reflect polymorphic strategies within the population, but rather that schools split and merge, contract and disperse, and change shape frequently (Misund et al. 1995; Pitcher et al. 1996; Mackinson et al. 1999). Schooling fish quickly respond to the attacks from predators, and variability in school size and packing density

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should vary with food availability and hunger (Morgan 1988; Robinson and Pitcher 1989*a*, 1989*b*). Packing density within schools is generally very heterogeneous, also including empty vacuoles that act as obstacles that fish in the back of the school also swim around (Freon et al. 1992; Misund 1993). Such vacuoles will represent small islands of survival for all potential prey within its volume.

Hierarchical aggregations

Patchiness of organisms is often hierarchical (Kotliar and Wiens 1990; Fauchald et al. 2000), where individuals are found within patches, which are found within clusters, etc. Such patterns have been described for a variety of animals, including both mesopelagic fish in scattering layers (Benoit-Bird and Au 2003) and epipelagic, scooling fish (Mackinson et al. 1999; Petitgas et al. 2001; Haugland and Misund 2004). Such hierarchical patch structure can be incorporated within the model framework presented here. Assuming that schools are randomly distributed subunits within clusters that move independently of each other

$$(25)\quad m_D = -\ln \sum_{Z=0}^{\infty}\sum_{Y=0}^{\infty}\sum_{X=0}^{\infty} e^{-lN_T \pi r^2 v_h} \frac{e^{-\hat{Z}}\hat{Z}^Y}{Z!} \frac{e^{-Yz}(\hat{Y}Z)^Y}{Y!}$$

where $\hat{Z}$, the average number of encounters with clusters per time, depends on the speed of the clusters and their size and interschool distance (cf. eq. 20). More generally, if predator patchiness is hierarchical, the probabilities of encountering different numbers of individual predators depend on the probabilities of encountering different numbers of schools, which again depend on the number of encounters with clusters. Hence

$$(26)\quad m_D = -\ln \sum_{Z=0}^{\infty}\sum_{Y=0}^{\infty}\sum_{X=0}^{\infty} \lambda^{-X} P(Z) P(Y|Z) P(X|Y, Z)$$

Predator population dynamics and prey mortality pattern

Predator population dynamics may result in variability in the size of the feeding area, the packing density or spatial extent of groups, or the density of groups, and according to the model predictions presented here, these possible scenarios have very different implications for the mortality regime of prey. For instance, the feeding migrations of Norwegian spring-spawning herring has changed remarkably during the last 50 years, and the size of the feeding area has declined and increased corresponding to the collapse and rebuilding of the stock (Holst et al. 2002). This means that during the decades of very low herring abundance, a small fraction of the zooplankton in the Nordic Seas experienced major predation from herring, while most experienced no herring at all. According to the model, as long as the population size has no effect on school sizes or packing density, population size should have no effect on the size dependency of imposed planktonic mortality. Variability in the abundance of schooling fish can, however, result in variability in the density of schools, school size, or packing density (Petitgas 1998; Castillo and Robotham 2004). Planktivores that are aggregated by topography and not from social behaviour will typically respond with a change in packing density when overall abundance changes. More detailed knowledge about the aggregative responses of planktivores to changes in their abundance is instrumental for our understanding of the mortality regime of plankton and fish larvae being preyed upon by planktivores that fluctuate in abundance.

Further model validation and development

The presented model relies on well-established predation mechanics, and its validity when its assumptions are valid is probably less of an open question than how important predator aggregation is in modulating vulnerability dependence of plankton mortality in real systems. Ideally, one should quantify (*i*) the predation risk of different prey imposed by individual predators experimentally, (*ii*) the remaining fractions of different prey after a body of water has been searched by a group of predators (as done by Koslow 1981), and (*iii*) the overall mortality rate of different prey populations (cf. Pepin et al. 2003). Such empirical results should then be contrasted with predictions from mechanistic models reflecting factual time budgets for predator space use and aggregation behaviour. When predators are not purely handling-limited, the presented model is not valid, as mortality rate changes as a feeding predator group progresses through a body of water. However, extending the presented model to include handling limitation can be done by calculating mortality rates for each prey class within short time intervals sequentially. Therefore, applying this approach to real systems where predators can be both handling- and encounter-limited is at least technically accomplishable.

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References

Aksnes, D.L., and Giske, J. 1990. Habitat profitability in pelagic environments. Mar. Ecol. Prog. Ser. **64**: 209–215.

Aksnes, D.L., and Giske, J. 1993. A theoretical model of aquatic visual feeding. Ecol. Model. **67**: 233–250.

Aksnes, D.L., and Utne, A.C.W. 1997. A revised model of visual range in fish. Sarsia, **82**: 137–147.

Aksnes, D.L., Nejstgaard, J., Sodberg, E., and Sornes, T. 2004. Optical control of fish and zooplankton populations. Limnol. Oceanogr. **49**: 233–238.

Bagøien, E., Kaartvedt, S., and Øverås, S. 2000. Seasonal vertical migrations of *Calanus* spp. in Oslofjorden. Sarsia, **85**: 299–311.

Bagøien, E., Kaartvedt, S., Eiane, K., and Aksnes, D.L. 2001. Vertical distribution and mortality of overwintering *Calanus*. Limnol. Oceanogr. **46**: 1494–1510.

Bailey, K.M., and Houde, E.D. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Adv. Mar. Biol. **25**: 1–83.

Benoit-Bird, K.J., and Au, W.W.L. 2003. Spatial dynamics of a nearshore, micronekton sound-scattering layer. ICES J. Mar. Sci. **60**: 899–913.

Burgess, J.W., and Shaw, E. 1979. Development and ecology of fish schooling. Oceanus, **22**: 11–17.

Castillo, J., and Robotham, H. 2004. Spatial structure and geometry of schools of sardine, (*Sardinops sagax*) in relation to abun-

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dance, fishing effort, and catch in northern Chile. ICES J. Mar. Sci. **61**: 1113–1119.

Dale, T., Bagøien, E., Melle, W., and Kaartvedt, S. 1999. Can predator avoidance explain varying overwintering depth of *Calanus* in different oceanic water masses? Mar. Ecol. Prog. Ser. **179**: 113–121.

Dalpadado, P., Ellertsen, B., Melle, W., and Skjoldal, H.R. 1998. Summer distribution patterns and biomass estimates of macroplankton and micronekton in the Nordic Seas. Sarsia, **83**: 103–116.

De Robertis, A. 2002. Size-dependent visual predation risk and the timing of vertical migration: an optimization model. Limnol. Oceanogr. **47**: 925–933.

Dodson, S.I. 1974. Adaptive change in plankton morphology in response to size-selective predation — new hypothesis of cyclomorphosis. Limnol. Oceanogr. **19**: 721–729.

Dommasnes, A., Melle, W., Dalpadado, P., and Ellertsen, B. 2004. Herring as a major consumer in the Norwegian Sea. ICES J. Mar. Sci. **61**: 739–751.

Drenner, R.W., Strickler, J.R., and O'Brien, W.J. 1978. Capture probability: the role of zooplankter escape in the selective feeding of planktivorous fish. J. Fish. Res. Board Can. **35**: 1370–1373.

Eggers, D.M. 1976. Theoretical effects of schooling by planktivorous fish predators on rate of prey consumption. J. Fish. Res. Board Can. **33**: 1964–1971.

Eggers, D.M. 1977. Nature of prey selection by planktivorous fish. Ecology, **58**: 46–59.

Fauchald, P., Erikstad, K.E., and Skarsfjord, H. 2000. Scale-dependent predator–prey interactions: the hierarchical spatial distribution of seabirds and prey. Ecology, **81**: 773–783.

Fiksen, Ø., and MacKenzie, B.R. 2002. Process-based models of feeding and prey selection in larval fish. Mar. Ecol. Prog. Ser. **243**: 151–164.

Freon, P., Gerlotto, F., and Soria, M. 1992. Changes in school structure according to external stimuli: description and influence on acoustic assessment. Fish. Res. **15**: 45–67.

Freon, P., and Misund, O.A. 1999. Dynamics of pelagic fish distribution and behaviour: effects on fisheries and stock assessment. Fishing News Books, Blackwell Science Limited, Oxford.

Genin, A. 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. J. Mar. Syst. **50**: 3–20.

Genin, A., Greene, C., Haury, L., Wiebe, P., Gal, G., Kaartvedt, S., Meir, E., Fey, C., and Dawson, J. 1994. Zooplankton patch dynamics: daily gap formation over abrupt topography. Deep-Sea Res. I, **41**: 941–951.

Giguere, L.A., and Northcote, T.G. 1987. Ingested prey increase risks of visual predation in transparent *Chaoborus* larvae. Oecologia, **73**: 48–52.

Giske, J., Huse, G., and Fiksen, Ø. 1998. Modelling spatial dynamics of fish. Rev. Fish Biol. Fish. **8**: 57–91.

Gliwicz, Z.M. 1986. Predation and the evolution of vertical migration in zooplankton. Nature (London), **320**: 746–748.

Godø, O.R., Hjellvik, V., Iversen, S.A., Slotte, A., Tenningen, E., and Torkelsen, T. 2004. Behaviour of mackerel schools during summer feeding migration in the Norwegian Sea, as observed from fishing vessel sonars. ICES J. Mar. Sci. **61**: 1093–1099.

Greene, C.H. 1986. Patterns of prey selection: implications of predator foraging tactics. Am. Nat. **128**: 824–839.

Hansen, B., Bjørnsen, P.K., and Hansen, P.J. 1994. The size ratio between planktonic predators and their prey. Limnol. Oceanogr. **39**: 395–403.

Haugland, E.K., and Misund, O.A. 2004. Evidence for a clustered spatial distribution of clupeid fish schools in the Norwegian Sea and off the coast of southwest Africa. ICES J. Mar. Sci. **61**: 1088–1092.

Haury, L., Fey, C., Gal, G., Hobday, A., and Genin, A. 1995. Copepod carcasses in the ocean. I. Over seamounts. Mar. Ecol. Prog. Ser. **123**: 57–63.

Haury, L., Fey, C., Newland C., and Genin, A. 2000. Zooplankton distributions around four eastern North Pacific seamounts. Prog. Oceanogr. **45**: 69–105.

Holst, J.C., Dragesund, O., Hamre, J., Misund, O.A., and Østvedt, O.J. 2002. Fifty years of herring migrations in the Norwegian Sea. ICES Mar. Sci. Symp. **215**: 352–360.

Houston, A.I., McNamara, J.M., and Hutchinson, J.M.C. 1993. General results concerning the trade-off between gaining energy and avoiding predation. Philos. Trans. R. Soc. Lond. B Biol. Sci. **341**: 375–397.

Hugie, D.M., and Dill, L.M. 1994. Fish and game: a game theoretic approach to habitat selection by predators and prey. J. Fish Biol. **45**(Suppl. A): 151–169.

Isaacs, J.D., and Schwartzlose, R.A. 1965. Migrant sound scatterers: interaction with the seafloor. Science (Washington, D.C.), **150**: 1810–1813.

Kaartvedt, S. 2000. Life history of *Calanus finmarchicus* in the Norwegian Sea in relation to planktivorous fish. ICES J. Mar. Sci. **57**: 1819–1824.

Kaartvedt, S., Knutsen, T., and Holst, J.C. 1998. Schooling of the vertically migrating mesopelagic fish *Maurolicus muelleri* in light summer nights. Mar. Ecol. Prog. Ser. **170**: 287–290.

Kaartvedt, S., Røstad, A., Fiksen, Ø., Melle, W., Torgersen, T., Breien, M., and Klevjer, T.A. 2005. Piscivores patrol krill swarms. Mar. Ecol. Prog. Ser. **299**: 1–5.

Koslow, J.A. 1981. Feeding selectivity of schools of northern anchovy, *Engraulis mordax*, in the Southern California Bight. Fish. Bull. **71**: 131–142.

Kotliar, N.B., and Wiens, J.A. 1990. Multiple scales of patchiness and patch structure — a hierarchical framework for the study of heterogeneity. Oikos, **59**: 253–260.

Lima, S.L. 2002. Putting predators back into behavioral predator prey interactions. Trends Ecol. Evol. **17**: 70–75.

Lima, S.L., and Bednekoff, P.A. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. Am. Nat. **153**: 649–659.

Lima, S.L., and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**: 619–640.

Mackinson, S., Nøttestad, L., Guénette, S., Pitcher, T., Misund, O.A., and Fernö, A. 1999. Cross-scale observations on distribution and behavioural dynamics of ocean feeding Norwegian spring-spawning herring. ICES J. Mar. Sci. **56**: 613–626.

Misund, O.A. 1993. Dynamics of moving masses: variability in packing density, shape, and size among herring, sprat, and saithe schools. ICES J. Mar. Sci. **50**: 145–160.

Misund, O.A., Aglen, A., and Frønæs, E. 1995. Mapping the shape, size, and density of fish schools by echo integration and a high resolution sonar. ICES J. Mar. Sci. **52**: 11–20.

Misund, O.A., Vilhjálmsson, H., Jákupsstovu, S.H., Røttingen, I., Belikov, S., Asthorsson, Blindheim, O.J., Jónsson, J., Krysov, A., Malmberg, S.A., and Sveinbjørnsson, S. 1998. Distribution, migration and abundance of Norwegian spring spawning herring in relation to the temperature and zooplankton biomass in the Norwegian Sea as recorded by coordinated surveys in spring and summer 1996. Sarsia, **83**: 117–127.

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Morgan, M.J. 1988. The effect of hunger, shoal size and the presence of a predator on shoal cohesiveness in bluntnose minnows, *Pimephales notatus* Rafinesque. J. Fish Biol. **32**: 963–971.

Paradis, A.R., and Pepin, P. 2001. Modelling changes in the length-frequency distributions of fish larvae using field estimates of predator abundance and size distributions. Fish. Oceanogr. **10**: 217–234.

Paradis, A.R., Pepin, P., and Brown, J.A. 1996. Vulnerability of fish eggs and larvae to predation: a review of the influence of the relative size of prey and predator. Can. J. Fish. Aquat. Sci. **53**: 1226–1235.

Paradis, A.R., Pepin, M., and Pepin, P. 1999. Disentangling the effects of size-dependent encounter and susceptibility to predation with an individual-based model for fish larvae. Can. J. Fish. Aquat. Sci. **56**: 1562–1575.

Pearre, S., Jr. 1980. Feeding by Chaetognatha: the relation of prey size to predator size in several species. Mar. Ecol. Prog. Ser. **3**: 125–134.

Pepin, P., Dower, J.F., Helbig, J.A., and Leggett, W.C. 2002. Estimating the relative roles of dispersion and predation in generating regional differences in mortality rates of larval radiated shanny (*Ulvaria subbifurcata*). Can. J. Fish. Aquat. Sci. **59**: 105–114.

Pepin, P., Dower, J.F., and Davidson, F.J.M. 2003. A spatially explicit study of prey–predator interactions in larval fish: assessing the influence of food and predator abundance on larval growth and survival. Fish. Oceanogr. **12**: 19–33.

Petitgas, P. 1998. Biomass-dependent dynamics of fish spatial distributions characterized by geostatistical aggregation curves. ICES J. Mar. Sci. **55**: 443–453.

Petitgas, P., Reid, D., Carrera, P., Iglesias, M., Georgakarakos, S., Liorzou, B., and Massé, J. 2001. On the relation between schools, clusters of schools, and abundance in pelagic fish stocks. ICES J. Mar. Sci. **58**: 1160–1150.

Pitcher, T.J., Misund, O.A., Fernö, A., Totland, B., and Melle, W. 1996. Adaptive behaviour of herring schools in the Norwegian Sea as revealed by high resolution sonar. ICES J. Mar. Sci. **53**: 449–452.

Reid, S.B., Hirota, J., Young, R.E., and Hallacher, L.E. 1991. Mesopelagic-boundary community in Hawaii: micronekton at the interface between neritic and oceanic systems. Mar. Biol. **109**: 427–440.

Ritz, D.A. 1994. Social aggregation in pelagic invertebrates. Adv. Mar. Biol. **30**: 155–216.

Robinson, C.J., and Pitcher, T.J. 1989*a*. The influence of hunger and ration level on shoal density, polarization and swimming speed of herring, *Clupea harengus* L. J. Fish Biol. **34**: 631–633.

Robinson, C.J., and Pitcher, T.J. 1989*b*. Hunger motivation as a promoter of different behaviours within a shoal of herring: selection for homogeneity in fish shoal? J. Fish Biol. **35**: 459–460.

Salvanes, A.G.V., Aksnes, D.L., and Giske, J. 1992. Ecosystem model for evaluating the potential cod production in a west Norwegian fjord. Mar. Ecol. Prog. Ser. **90**: 9–22.

Scharf, F.S., Buckel, J.A., Juanes, F., and Conover, D.O. 1998. Predation by juvenile piscivorous bluefish (*Pomatomus saltatrix*): the influence of prey to predator size ratio and prey type on predator capture success and prey profitability. Can. J. Fish. Aquat. Sci. **55**: 1695–1703.

Titelman, J., and Fiksen, Ø. 2004. Ontogenetic vertical distribution patterns in small copepods: field observations and model predictions. Mar. Ecol. Prog. Ser. **284**: 49–63.

Torgersen, T., Kaartvedt, S., Melle, W., and Knutsen, T. 1997. Large scale distribution of acoustical scattering layers at the Norwegian continental shelf and the eastern Norwegian Sea. Sarsia, **82**: 87–96.

Tsuda, A., Saito, H., and Hirose, T. 1998. Effect of gut content on the vulnerability of copepods to visual predation. Limnol. Oceanogr. **43**: 1944–1947.

Utne-Palm, A.C. 2000. Prey visibility, activity, size and catchability's (evasiveness) influence on *Gobiosculus flavescens* prey choice. Sarsia, **85**: 157–165.

Varpe, Ø., Fiksen, Ø., and Slotte, A. 2005. Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. Oecologia, **146**: 443–451.

Vinyard, G.L. 1980. Differential prey vulnerability and predator selectivity: effects of evasive prey on bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) predation. Can. J. Fish. Aquat. Sci. **37**: 2294–2299.

Wolanski, E., and Hamner, W.M. 1988. Topographically controlled fronts in the ocean and their biological influence. Science (Washington, D.C.), **241**: 177–181.

Zaret, T.M., and Suffern, J.S. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnol. Oceanogr. **21**: 804–813.

List of symbols

b body length of prey (mm)
D domain
E visual capacity parameter
I predator feeding rate (prey-predator^{-1}-time^{-1})
k light extinction coefficient (m^{-1})
K_E light half-saturation parameter (microEinstein, μE)
l length of predator group (distance)
m instantaneous mortality rate (time^{-1})
m_D m averaged over D (time^{-1})
$m_{D_{dep}}$ m_D imposed by dependent predators (time^{-1})
$m_{D_{indep}}$ m_D imposed by independent predators (time^{-1})
m_T m per $T < T_{tot}$ (time^{-1})
$m_{T_{tot}}$ m per $T_{tot} > T$ (time^{-1})
n prey density (prey-space^{-1})
N predator density (predators-space^{-1})
N_D average predator density in D (predators-space^{-1})
N_g N within group (predators-space^{-1})
N_G predator group density (predator groups-space^{-1})
N_s N in habitat s (predators-space^{-1})
$N_{T_{tot}}$ N averaged over T_{tot} (predators-space^{-1})
p_{surv} survival probability per time (time^{-1})
p_{surv_D} p_{surv} averaged over D (time^{-1})
p_{surv_s} p_{surv} in habitat s (time^{-1})
$p_{surv_{Y_{dep}}}$ p_{surv} if encountering Y dependent groups (time^{-1})
$p_{surv_{Y_{indep}}}$ p_{surv} if encountering Y independent groups (time^{-1})
q_s probability of being in habitat s
r search range (distance)
s habitat in D
S number of different habitats in D
t retention time of group (time)
T time interval < T_{tot} (time)
T_{tot} time interval > T (time)
u velocity (distance-time^{-1})
V search rate (space-time^{-1}-predator^{-1})
V_G group search rate (space-time^{-1})
X encounter rate with predators (predators-time^{-1})
$\bar{X}$ average X (predators-time^{-1})

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Y encounter rate with predator groups (predator groups-time^{-1})
$\hat{Y}$ average Y (predator groups-time^{-1})
Z encounter rate with predator clusters (predator clusters-time^{-1})
$\hat{Z}$ average Z (predator clusters-time^{-1})
λ capture efficiency of predator
λ_G λ of a predator group
$\lambda_{G_{dep}}$ λ_G of a dependent group
$\lambda_{G_{indep}}$ λ_G of an independent group

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Simplification of seagrass food webs across a gradient of nutrient enrichment

Alexander Tewfik, Joseph. B. Rasmussen, and Kevin S. McCann

Abstract: Anthropogenic nutrient enrichment has resulted in significant changes in food web structure. Although such changes have been associated with the loss of diversity and ecosystem services, little empirical work has been done to study food webs of similar systems across a nutrient enrichment gradient. We examined 11 seagrass beds along a gradient of increasing $\delta^{15}N$ of primary consumers, where $\delta^{15}N$ is used as an indicator of sewage-derived nutrients. Observations across this gradient revealed corresponding increases in consumer density and changes in distinct functional groups, whereas consumer diversity, seagrass canopy, and macrodetrital biomass decreased. However, maximum overall primary consumer diversity and minimum density occurred at intermediate levels along the nutrient gradient. We hypothesize that higher species diversity at low to moderate levels of nutrient enrichment depends on the persistence of grazer-resistant seagrass. This seagrass canopy, and the significant macrodetritus it generates, facilitates a variety of food and shelter resources. Overgrazed and simplified habitats may occur when densities of generalist urchins, capable of direct producer consumption, are no longer controlled through competition, predation, and intraguild predation. We hypothesize that high and stable urchin populations appear possible with the increased availability of allochthonous phytoplankton and associated particulate detritus that is a well-known consequence of nutrient enrichment in aquatic systems.

Résumé : L'enrichissement anthropique en nutriments a produit des changements significatifs dans les réseaux alimentaires. Bien que de tels changements soient souvent associés à une perte de diversité et de services dans les écosystèmes, on a fait peu d'études empiriques sur les réseaux alimentaires de systèmes semblables le long d'un gradient d'enrichissement en nutriments. Nous avons examiné 11 herbiers marins dans un gradient de valeurs croissantes de $\delta^{15}N$ des consommateurs primaires, dans lequel $\delta^{15}N$ sert d'indice de l'importance des nutriments provenant des égouts. Des observations le long de ce gradient montrent des accroissements correspondants de la densité des consommateurs et des changements dans certains groupes fonctionnels, alors que la diversité des consommateurs, la couverture d'herbes marines et la biomasse du macrodétritus diminuent. Cependant, la diversité maximale et la densité minimale globales des consommateurs primaires se retrouvent dans les niveaux intermédiaires du gradient de nutriments. Nous émettons l'hypothèse selon laquelle la diversité spécifique plus élevée observée aux niveaux bas et intermédiaires d'enrichissement en nutriments dépend de la persistance d'herbes marines résistantes aux brouteurs. Cette couverture d'herbes marines et l'important macrodétritus qu'elle produit favorisent une variété de ressources alimentaires et de refuges. Des habitats surexploités et simplifiés peuvent se développer lorsque les oursins généralistes, capables de consommer directement les producteurs, ne sont plus contrôlés par la compétition, la prédation générale et la prédation à l'intérieur de leur guilde. Notre hypothèse veut qu'il soit possible d'obtenir des populations fortes et stables d'oursins lorsqu'il y a un accroissement de la disponibilité du phytoplancton allochtone et du détritus particulaire associé, ce qui est une conséquence bien connue de l'enrichissement en nutriments dans les écosystèmes aquatiques.

[Traduit par la Rédaction]

Introduction

A number of researchers have highlighted how widespread anthropogenic disturbances, in particular nutrient loading, often leads to drastic changes in ecosystems (Hughes 1994; Jackson 2001; Scheffer et al. 2001). More importantly, they have found evidence that once the ecosystem is altered, it may become very difficult to return the system back to its original state by simply reducing perturbations (Scheffer et al. 2001). The "catastrophe" ecosystem theory that emerges from this research suggests that major functional groups in the food web also change dramatically and in doing so drive ecosystem level changes that feed back to maintain the system in this new altered state. As an example, lake research-

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ers have found that eutrophication of small lakes initiates a switch from benthic to pelagic (i.e., phytoplankton) dominated production, frequently flipping the lake from a clear state to a turbid state (Carpenter et al. 1999; Vadeboncoeur et al. 2003). Among other physical changes, this turbid lake state diminishes light penetration, possibly preventing benthic macrophytes of the clear lake state from returning. Such examples suggest that we must begin to understand how food web structure and function are altered across environmental gradients, especially gradients that reflect human development through time (e.g., nutrient loading, fragmentation, etc.).

Coastal marine ecosystems may be especially prone to the effects of human development as urbanization, organic runoff, and associated nutrient loading tend to be most dramatic on coasts (McClelland et al. 1997; Cloern 2001). As with lakes, increased nutrient inputs may play a major role in restructuring the food web. Recent theory on the role of such inputs (i.e., allochthonous forms) suggests that generalist consumers frequently tap into these alternative energy supplies, fuelling significant changes in the dominance of species in these food webs (Polis and Strong 1996). A well-documented example of this phenomenon is seen by the tremendous influence of migrating snow geese (*Chen caerulescens caerulescens*) on the Hudson Bay lowlands (Jefferies 2000). Geese have exploited agricultural subsidises in winter feeding areas leading to increases in populations. Subsequent negative effects of the subsidy are seen in the fragile summer staging, nesting, and brooding areas with loss of vegetation, declines in shorebird densities, and losses of soil invertebrate assemblages (Jefferies et al. 2004). Furthermore, the donor-controlled aspect (i.e., consumers not affecting resource renewal rate) of these interactions with generalist consumers may frequently be stable (Huxel and McCann 1998), despite the fact that increased generalist consumer density drives heightened suppression (e.g., overgrazing) of important autochthonous resources (e.g., detritus).

In addition, food web ecologists have largely ignored the role that detrital pathways play in the diversity and structuring of food webs (Polis and Strong 1996; Moore et al. 2004). Detritus and associated pathways form rich alternative energy sources, drive nutrient recycling, and provide complex habitat structure that should influence diversity, community structure, and dynamics (Wetzel 1995; Moore et al. 2004). Food web ecology lacks a well-developed theory for the role of detritus (although see DeAngelis 1992), yet few empirical studies have been carried out to elucidate the patterns in detritus-based food web structure of ecosystems.

The extensive exploitation of marine species within the Caribbean seagrass – coral reef – mangrove habitat complex over the last three centuries has resulted in major changes in food web structure (Hughes 1994; Jackson et al. 2001). More recently, nutrient loading resulting from increases in human populations and associated urbanization along coastlines has also been identified as a significant issue in the degradation of Caribbean marine habitats (Duarte 1995; Short and Wyllie-Echeverria 1996; Jackson 2001). During this same period, the generalist herbivorous urchin *Lytechinus variegatus* has been observed overgrazing detritus and living seagrass (Camp et al. 1973; Valentine and Heck 1991; Rose et al. 1999). The loss of traditional seagrass systems, known to support structurally complex detritus-based food webs, would negatively affect species diversity and a number of ecosystem services (Short and Wyllie-Echeverria 1996). Such services include their use as nursery and foraging habitats, nutrient recycling, sediment stabilization, and export of significant production to mangroves, coral reef, and open-ocean food webs (Jackson 2001; Duarte 2002).

Perhaps because of the limited nature of food web data, little effort has been spent on comparing food webs of a similar system across environmental or disturbance gradients. However, such empirical analysis could significantly aid in our understanding of how ecosystems and food webs change with respect to modern anthropogenic influences (McCann 2007). In this study, we will examine the response of seagrass food web structure along a gradient of nutrient enrichment. Such a gradient may indeed encompass other historical disturbances (i.e., overfishing), with coastal eutrophication being perhaps the most significant anthropogenic process occurring in coastal waters (McClelland et al. 1997; Grall and Chauvaud 2002). We show increases in the level of $\delta^{15}N$ enrichment within components of seagrass food webs as a function of human population densities within watersheds. Such enrichment is consistent with high levels of wastewater, including organic matter and inorganic nutrients, being delivered from watersheds to nearshore ecosystems. We then empirically consider how altered nutrient levels correlate to attributes of seagrass community structure, including abundance of benthic resources, with special attention to seagrass macrodetritus and mega-invertebrate consumer functional groups. We will show that seagrass communities become greatly simplified or homogenized with increased nutrients such that these impacted ecosystems have reduced seagrass canopies, little, if any, seagrass detritus, low animal diversity, and substantially increased densities of generalist consumers (i.e., sea urchins).

Materials and methods

Human populations and nutrient enrichment

The enrichment of the naturally occurring heavy isotope of nitrogen (^{15}N) from food source to consumer allows the trophic position of organisms from a wide variety of taxa to be determined with reasonable confidence (Peterson and Fry 1987). Consumers acquire stable isotope signatures through their diet, with nitrogen stable isotope ($\delta^{15}N$) pools of animals enriched by 3.4‰ ± 0.3‰ relative to their diet (Minagawa and Wada 1984; Peterson and Fry 1987).

In the past, comparisons of trophic structure across systems were complicated by variation in $\delta^{15}N$ at the base of food webs. The C:N of diets, form of nitrogenous waste excreted, and other sources of variation may yield differences in $\delta^{15}N$ fractionation, although the exact mechanism of this variation and the direction of such change remains unclear (Adams and Sterner 2000; Vanderklift and Ponsard 2003). However, among-lake comparisons of large and long-lived primary consumers have illustrated that $\delta^{15}N$ increases significantly with human population densities in watersheds (Cabana and Rasmussen 1996). The high trophic position of humans, expressed through sewage-derived nutrients as well as enrichment due to microbial processing, is reflected in the

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receiving bodies of water and resident organisms at all trophic levels. Various studies now suggest strong links between land use in watersheds and benthic food webs (producers and consumers) and specifically that $\delta^{15}N$ values may be used as suitable indicators in the detection and relative quantification of increases in sewage-derived nutrients (McClelland et al. 1997; Cole et al. 2004; Martinetto et al. 2006). In fact, labile nutrient concentrations (e.g., nitrate and phosphate) may not indicate significant differences across well-documented gradients of eutrophication (Green and Webber 2003). Therefore, for the remainder of this paper, we assume that increases in $\delta^{15}N$ enrichment of primary benthic consumers are consistent with increases in sewage-derived nutrient enrichment to coastal habitats that is a function of increasing human population densities in watersheds. We have therefore used the $\delta^{15}N$ signal of long-lived, ubiquitous benthic primary consumers (e.g., *Pinna carnea*, *Lytechinus variegatus*, *Oreaster reticulates*, *Strombus gigas*) of limited mobility to establish a gradient of nutrient enrichment across 11 sites in Barbados, Dominican Republic, and Panama (Table 1), where we examined attributes of seagrass communities. These sites were haphazardly chosen from accessible locations and represent a range of commonly observed conditions across the region. Human population densities, correlated with $\delta^{15}N$ signals, were calculated using watershed areas and human population from the best available topographic and population maps, as well as government census data. This relationship was tested for significance using statistical components of Sigmaplot 2001 version 7.0 (SYSTAT 2001). Additional sites in the Dominican Republic ($N = 2$) and Haiti ($N = 2$) were examined only for $\delta^{15}N$ signatures of benthic producers and consumers in relation to human populations in adjacent settlements because of logistical constraints. A further five sites were eliminated because of sediment runoff induced zero visibility or high wave energies (see below).

Tissue samples of invertebrates were collected during transect surveys. Muscle tissue was sampled from molluscs, and soft tissues were extracted from echinoderms. All samples were dried for 24 h at 80 °C, ground to a fine powder, and packed into 4 mm × 6 mm tin capsules. Stable isotope analyses were performed on a mass spectrometer at the G.G. Hatch Laboratories, Department of Earth Sciences, University of Ottawa (Ottawa, Ontario). Replicate samples ($N = 24$) showed good technical precision for $\delta^{15}N$ signals (standard deviation (SD) = 0.19‰).

Community structure across the gradient

Macrophyte biomass and mega-invertebrate density surveys were conducted using transects and quadrats in 11 distinct seagrass beds in Barbados ($N = 1$), Dominican Republic ($N = 7$), and Panama ($N = 3$) (Table 1). All sites encompassed large areas of seagrass habitat within several hundred metres of the coast and were selected to reduce the influence of acute physical disturbance (i.e., wave energies). This was accomplished by avoiding the three highest wave exposure categories in which coasts are exposed to strong prevailing winds and (or) long fetch with little if any offshore break (Hiscock 1996). Where such physical disturbances are frequent and (or) intense, top-down and bottom-up forces may become relatively unimportant in structuring the community. Specifically, intense flushing by wave actions may significantly reduce the influence of increased nutrients. Standardized, 60 × 3 m transects, two to six per site, were conducted using SCUBA or snorkel within the seagrass beds in depths of 2–7 m. Macrophyte biomass and associated detritus was measured within 0.0625 m^2 (0.25 × 0.25 m) quadrats placed at 20, 40, and 60 m along each transect. All aboveground macrodetritus (up to 1 cm^2) and living macrophytes (seagrass (*Thalassia testudinum*, *Syringodium filiforme*); macroalgae (various genera, e.g., *Halimeda*, *Penicillus*, *Avrainvillea*)) were hand-collected, separated, dried for approximately 24 h at 80 °C, weighed (±0.01 g), and expressed as grams dry mass per square metre (g DM·m^{-2}) and percent biomass.

Mega-invertebrate densities (number of individuals per hectare) were determined within the transect area of 180 m^2 by carefully searching through macrophytes and surface sediments. Consumer diversity indices were calculated using the Shannon ($\log_e$) and Simpson ($1 - \lambda$) methods. Consumer functional feeding groups were established as follows: (*a*) epiphyte – detrital specialist, gastropods (*Strombus gigas*, *S. costatus*, *S. raninus*, *S. pugilus*); (*b*) generalist herbivores, regular urchins (*Lytechinus variegatus*, *Tripneustes ventricosus*, *Diadema antillarium*); (*c*) subsurface deposit feeders (irregular urchin *Meoma ventricosa*, sand dollars); (*d*) surface deposit feeders (sea star *Oreaster reticulatus*, sea cucumbers), and (*e*) suspension feeders (bivalve *Pinna carnea*, benthic jellyfish *Cassiopeia* spp.). Although some invertebrate predators–scavengers (gastropods *Murex* spp., *Pleuroploca gigantean*) were encountered and included in the calculations of diversity, low abundances overall (<0.22% of total mega-invertebrate abundance) precluded the construction of useful patterns of distribution across the nutrient gradient.

Regressions and model fitting

All regressions of resources and consumers, including consumer abundance and diversity, were made across the gradient of increasing nutrient enrichment established from mean $\delta^{15}N$ values of *Pinna carnea* at sites as a function of human population density (Table 1). Regressions were made using arcsine square root transformed percentages of resource biomass (g DM·m^{-2}) and consumer density (individuals·ha^{-1}), as well as log-transformed resource biomass (g DM·m^{-2}) and consumer density (individuals·ha^{-1}). This double analysis was undertaken to address the potential problems of constraints in the covariance and correlation structure and subsequent interpretation linked to the use of compositional data (Jackson 1997). However, given the fact that similar patterns were established using both types of data, only the compositional data are presented. Statistical evaluations of regressions were made using Sigmaplot 2001 version 7.0 (SYSTAT 2001). Because many of our regressions showed potential for parabolic behaviour, we fit all regressions using both linear and quadratic equations and then employed an F test of significance of the quadratic term (Zar 1999). These statistical evaluations, F = [(regression sum of squares (SS) for quadratic model – regression SS for linear model)/residual mean squares for quadratic model], were done using data extracted from Sigmaplot 2001 version 7.0 (SYSTAT 2001), the sig-

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Table 1. Site descriptions including location (B, Barbados; DR, Dominican Republic; P, Panama), human population density (individuals (ind.)·km^{-2}) within adjacent watersheds, number of transects surveyed, and mean δ^{15}N (± standard error (SE)) for representative suspension feeder (*Pinna carnea*), generalist grazer (*Lytechinus variegatus*), deposit feeder (*Oreaster reticulatus*), and specialist grazer (*Strombus gigas*).

				P.carnea			*L. variegatus*			*O. reticulatus*			*S. gigas*		
Site and location	Code	Humans (ind.·km^{-2})	Transects (*N*)	δ^{15}N	SE	*N*	δ^{15}N	SE	*N*	δ^{15}N	SE	*N*	δ^{15}N	SE	*N*
Punta Chimanche, Pedernales	DR9	1	6	2.99	0.32	2				1.00		1			
Baie Rousel, Pedernales	DR7	1	5	3.08	0.09	2							1.75	0.09	3
Bahia de las Aguilas, Pedernales	DR6	1	6	3.34	0.30	4	2.46	0.22	7	1.14	0.27	4	1.74	0.09	12
Puerto de la Alcoa (outer marker)	DR8	17	6	3.29	0.18	2				2.70		1			
Puerto de la Alcoa (south of pier)	DR5	17	6	3.88	0.06	2				2.79	0.47	2	2.28		1
Puerto de la Alcoa (north of pier)	DR4	17	2	4.22	0.14	2							4.28		1
Solarte Sur, Bocas del Toro	P4	25	3	4.62	0.01	2	2.44	0.02	2						
Bastimentos, Bocas del Toro	P2	25	2	4.83	0.31	2	2.56	0.12	2						
Smithsonian dock, Bocas del Toro	P1	827	2	4.68	0.08	2	4.97	0.01	2	5.43	0.05	2			
Barabona (inner harbour)	DR2	1110	6	6.15	0.19	4	6.57	0.31	7	5.04	0.32	4	5.85	0.27	5
St. Lawrence, south coast	B2[a]	2632	2				6.45[b]	0.15	2						
Total (*N*)				10			6			6			5		
R^2				0.75			0.81			0.99			0.85		
P				0.001			0.014			<0.0001			0.026		

Note: *N*, sample size; R^2, correlation coefficient of δ^{15}N of consumers and density of human populations; *P*, level of significance.

[a]Correlation between *P. carnea* and *L. variegatus* δ^{15}N values ($N = 14$) across five sites was significant ($R^2 = 0.62$, $P < 0.0008$); therefore mean value of *L. variegatus* was used in the absence of *P. carnea* at site B2.

[b]Another generalist grazer (*Tripneustes ventricosus*) also displayed elevated δ^{15}N of 6.61 ± 0.5 ($N = 7$).

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nificant ($P < 0.05$) results of which are presented as part of the figure captions.

Multivariate analysis

Nonmetric multidimensional scaling (nMDS), generated from a Bray–Curtis similarity matrix, was used to describe changes in arcsine square root transformed consumer functional group compositional data (% individuals·ha^{-1}) across the nutrient enrichment gradient (Clarke and Warwick 2001). The arrangement of abundance data (i.e., transects) has points most similar in functional group composition clustered together. Permutation-based hypothesis testing (analysis of similarity, ANOSIM) was used to detect differences within and between clusters of transects defined a priori as being exposed to low (<4), moderate (4–6), and high (>6) levels of enrichment based on mean δ^{15}N values of *Pinna carnea* at a site. The key outcome of ANOSIM is the *R* statistic, which ranges between –1 and +1, with a value of zero indicating that no difference between two groups is likely. Subsequently, similarity percentages (SIMPER) was used to identify consumer functional groups that provide similarity within a cluster and primary discrimination between two observed sample clusters (Clarke and Warwick 2001). Finally, the environmental variables (i.e., arcsine square root transformed macrophyte and associated detritus biomass data, g DM·m^{-2}) that best explained the observed patterns of consumer functional group composition were accomplished by maximizing a Spearman rank correlation between the Bray–Curtis similarity matrix for consumers and the Euclidian distance matrix for resources (BEST). All multivariate analyses described above were completed using PRIMER version 6.1.4 (Clarke and Gorley 2006).

Results

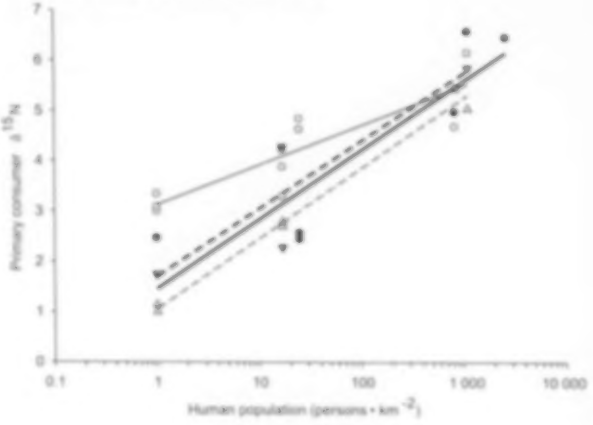
Nutrient enrichment gradient

A substantial and significant ($P < 0.026$) increase in δ^{15}N occurs within tissues of benthic organisms as human population density increases (Fig. 1). The strong positive relationship holds true for representatives of a number of benthic primary consumer functional groups (Fig. 1; Table 1). This pattern likely reflects the high levels of wastewater, including organic matter and inorganic nutrients, being delivered from the adjacent watershed to nearshore zones and is in good agreement with previous studies (McClelland et al. 1997; Cole et al. 2004; Martinetto et al. 2006). Hence, perhaps not surprisingly, high human densities are strongly correlated to high levels of nutrient enrichment. In addition, a number of other sites in the Dominican Republic and Haiti, where quantitative benthic surveys were not possible because of logistical constraints, displayed increasing δ^{15}N signatures of benthic producers and consumers with increasing urbanization and human populations (Table 2).

Community structure across the gradient — regression analyses

At the broadest level, fairly distinct patterns emerge among mega-invertebrate density and diversity across the nutrient enrichment gradient. First, an obvious and dramatic increase in total mega-invertebrate consumer density (log(total individuals·ha^{-1})) is apparent (Fig. 2*a*). These densities are extraordinarily high, peaking at over 163 000 individuals·ha^{-1} and comparable with other examples of runaway consumers studied in the literature (Rose et al. 1999; Jefferies 2000). Such high grazer densities are accompanied by a strong decrease in the overall diversity of mega-invertebrate consumers (Fig. 2*b*). The maximum mega-invertebrate consumer diversity and minimum density both occurred at intermediate levels along the nutrient gradient.

Fig. 1. Variation in δ^{15}N of primary consumers at 11 seagrass sites versus human population density (persons·km^{-2}) within adjacent watersheds. Consumers represent various functional groups: *Pinna carnea* (suspension feeder, open circle, thin solid line; $R^2 = 0.75$, $P = 0.0012$); *Lytechinus variegatus* (generalist grazer, solid circle, thick solid line; $R^2 = 0.81$, $P = 0.014$); *Oreaster reticulatus* (deposit feeder, open triangle, thin broken line; $R^2 = 0.99$, $P < 0.0001$); and *Strombus gigas* (specialist grazer, solid triangle, thick broken line; $R^2 = 0.85$, $P = 0.026$). Values used for site B2 are *L. variegatus* as no *P. carnea* was found. Watershed areas and associated human populations were calculated with the best available topographic and population maps, as well as government census data. Overlapping values for *y* axis may obscure some data points.



To further explore these patterns, we first examine the relative changes in the percent composition of benthic resources across our nutrient gradient (Fig. 3). At low nutrient enrichment, secondarily colonizing *Syringodium* is mixed with the "climax" seagrass *Thalassia* and associated macrodetritus (Figs. 3*a*–3*c*). The increase in consumer abundance at higher nutrient enrichment (Fig. 2*a*) is accompanied by a dramatic decrease in the relative composition of seagrass macrodetritus and *Syringodium* (Figs. 3*a*, 3*b*), whereas *Thalassia*, known to be less edible because of structural components including lignin (Cebrian and Duarte 1998), was found to increase significantly (Fig. 3*c*). No significant trends in macroalgae biomass were observed (Fig. 3*d*).

The detailed patterns of relative changes in the percent consumer composition superimposed on that of the benthic resources finds competitive specialists declining dramatically while generalist consumers ultimately increase and become dominant (Figs. 4*a*, 4*b*). This suggests that generalist consumers may be better able to utilize alternative resources (i.e., opportunistic autotrophs) that increase production in the anthropogenic-induced eutrophic environment. Further,

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Table 2. Mean $\delta^{15}N$ for a species of seagrass (*Thalassia testudinum*, single samples), seagrass epiphytes (single samples), and two generalist grazers (*Lytechinus variegates*, $N = 2$; *Tripneustes ventricosa*, $N = 2$) collected at four additional sites around the island of Hispaniola where no visual community composition transect data were possible to collect.

Site and location	Population	*Thalassia*	Epiphytes	*L. variegatus*	*T. ventricosus*
Lambi, outer Port-au-Prince harbour	4 000	1.72	2.4	3.81	5.03
Labadie, Northern Haiti (near cruise-ship port)	5 000	1.75	3.48	4.22	5.93
Las Galeras, northeast Dominican Republic	10 000	3.26	3.14	5.38	7.62
Puerto Plata, north coast Dominican Republic	111 000	4.76	4.2		8.63

Note: Human population data are estimates based on most recent census data.

Fig 2. Relationships of (*a*) mega-invertebrate density (log(total individuals·ha^{-1}), $R^2 = 0.75$, $P < 0.005$) and (*b*) mega-invertebrate diversity (open circle; Shannon (solid line), $R^2 = 0.75$, $P < 0.005$; solid circle; Simpson (broken line), $R^2 = 0.75$, $P < 0.005$) along a gradient of primary consumer $\delta^{15}N$ at 11 sites in Barbados, Dominican Republic, and Panama (based on mean $\delta^{15}N$ of *Pinna carnea* at each site). Error bars represent ±1 standard error. Quadratic fits were significantly different ($P < 0.05$) from linear model for (*a*) $F_{[0.05,1,10]} = 10.72$, (*b*, Shannon) $F_{[0.05,1,10]} = 11.76$, and (*b*, Simpson) $F_{[0.05,1,10]} = 11.97$.

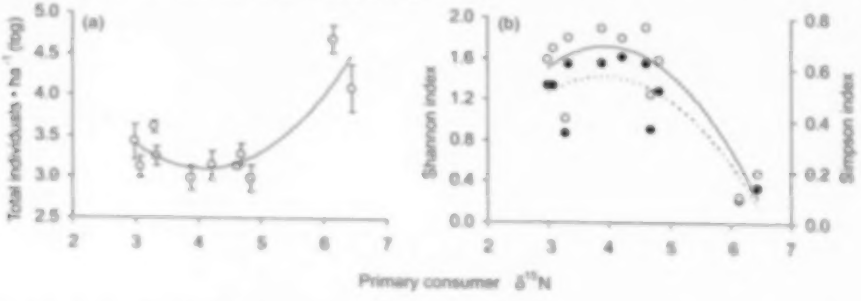
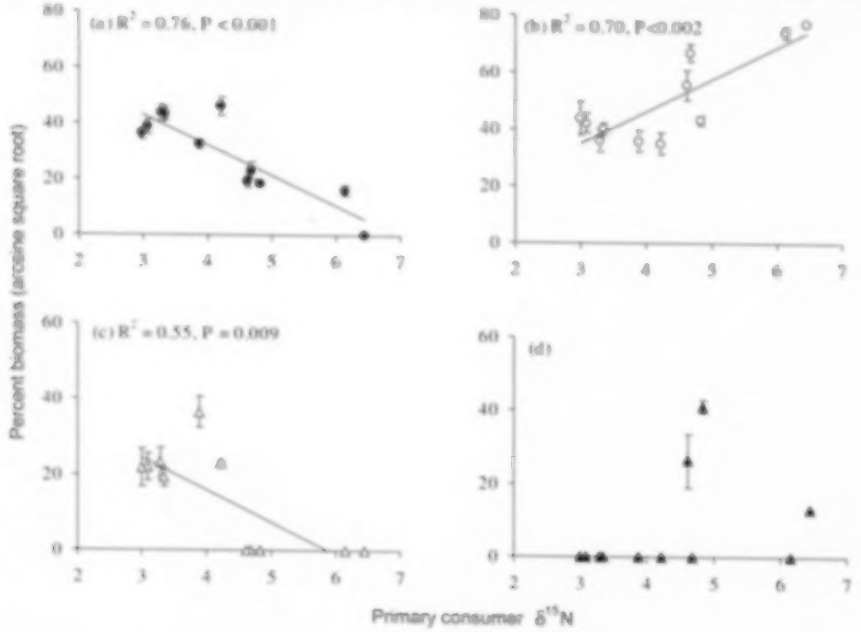


Fig 3. Percent biomass (g dry mass (DM)·m^{-2}) of resources (arcsine square root transformed) along a gradient of primary consumer $\delta^{15}N$ at 11 sites in Barbados, Dominican Republic, and Panama (based on mean $\delta^{15}N$ of *Pinna carnea* at each site). Resources: (*a*) detritus; (*b*) *Thalassia testudinum*; (*c*) *Syringodium filiforme*; and (*d*) Macroalgae (no significant regression observed). Error bars represent ±1 standard error.



as nutrient inputs begin to increase and the origins and types of detritus change (benthic to pelagic), subsurface deposit feeders also decline (Fig. 4*c*). Simultaneously, both surface deposit feeders (Fig 4*d*) and suspension feeders (Fig. 4*e*) first increase, peaking at intermediate nutrient levels, before decreasing when enrichment is high and opportunistic gener-

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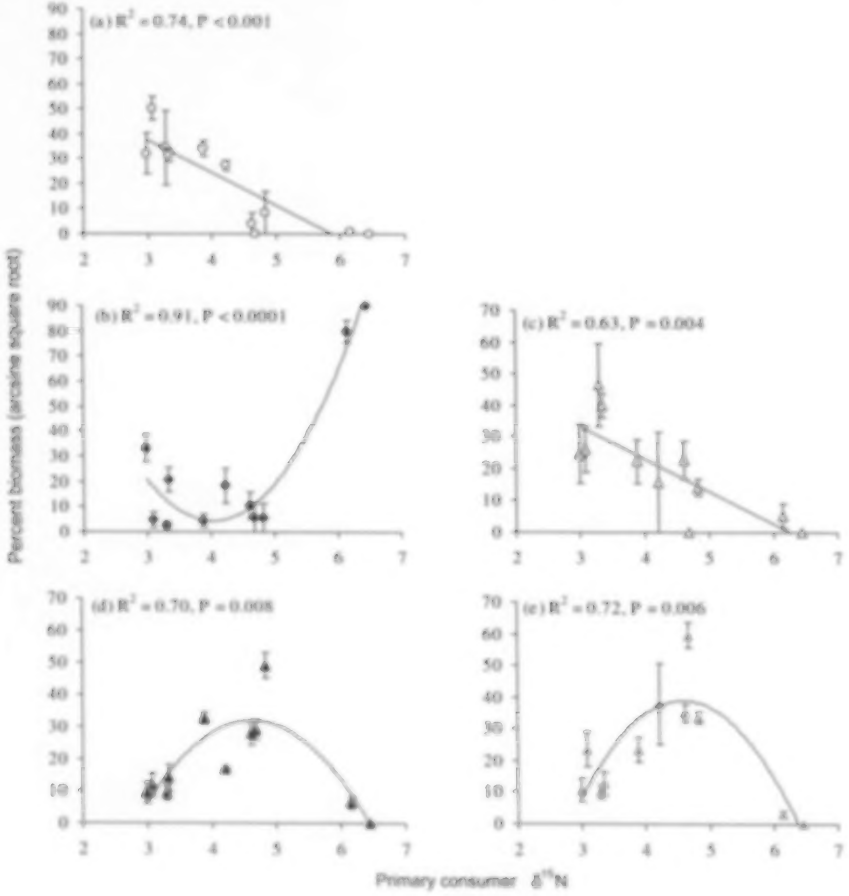
Fig. 4. Percent mega-invertebrate consumer density (arcsine square root transformed) along a gradient of primary consumer $\delta^{15}N$ at 11 sites in Barbados, Dominican Republic, and Panama (based on mean $\delta^{15}N$ of *Pinna carnea* at each site). Consumer functional groups are as follows: (*a*) specialists (*Strombus gigas*, *S. costatus*, *S. raninus*, *S. pugilus*); (*b*) generalists (*Lytechinus variegatus*, *Tripneustes ventricosus*, *Diadema antillarium*); (*c*) subsurface deposit feeders (*Meoma ventricosa* and sand dollars); (*d*) surface deposit feeders (*Oreaster reticulates* and sea cucumbers); and (*e*) suspension feeders (*Pinna carnea*, *Cassiopea* spp.). Error bars represent ±1 standard error. Quadratic fits were significantly different ($P < 0.05$) from linear model for (*b*) $F_{[0.05,1,10]} = 33.6$, (*d*) $F_{[0.05,1,10]} = 19.1$, and (*e*) $F_{[0.05,1,10]} = 20.33$.


(a) $R^2 = 0.74$, $P < 0.001$
(b) $R^2 = 0.91$, $P < 0.0001$
(c) $R^2 = 0.63$, $P = 0.004$
(d) $R^2 = 0.70$, $P = 0.008$
(e) $R^2 = 0.72$, $P = 0.006$
Percent biomass (arcsine square root)
Primary consumer $\delta^{15}N$

alist echinoids are most abundant (>66 000 individuals·ha^{-1}). It is worth noting a range of low density in generalist echinoids (Fig. 4*b*) corresponding to peaks in both surface deposit feeders and suspension feeders at intermediate ranges of enrichment.

Multivariate analyses

The primary consumer functional group communities along the nutrient gradient are spatially separated on the nMDS plot into low, moderate, and high enrichment clusters (Fig. 5). Significant differences between the three a priori defined groups of sites were found (Global $R = 0.879$, $P = 0.001$). The low enrichment sites were significantly different from the moderate ($R = 0.756$, $P = 0.008$) and high ($R = 1.000$, $P = 0.048$) sites.

Average similarities (SIMPER) within the three enrichment clusters were 79.8%, 72.6%, and 90.6% for low, moderate, and high enrichment clusters, respectively. Furthermore, each enrichment cluster's similarity was dominated by different consumer functional groups (Fig. 5). Finally, the BEST routine revealed that detritus biomass alone explained 58% of the pattern of consumer functional group abundance across the gradient, whereas a combination of detritus and *Thalassia* biomass gave the best overall explanation (>66%). Finally, the absolute mean values for the suite of benthic macrophyte resources (macrodetritus, *Thalassia*, *Syringodium*) are all quite different for each of the nutrient enrichment clusters (Fig. 5). The total biomass of macrophytes, including macrodetritus, declines, whereas the *Thalassia* component is largely maintained (Fig. 5). These gradual losses within the seagrass canopy begin to remove important habitat structure and food resources. These results also suggest a compensatory response by *Thalassia* to the increased nutrient additions and consumptive pressure on

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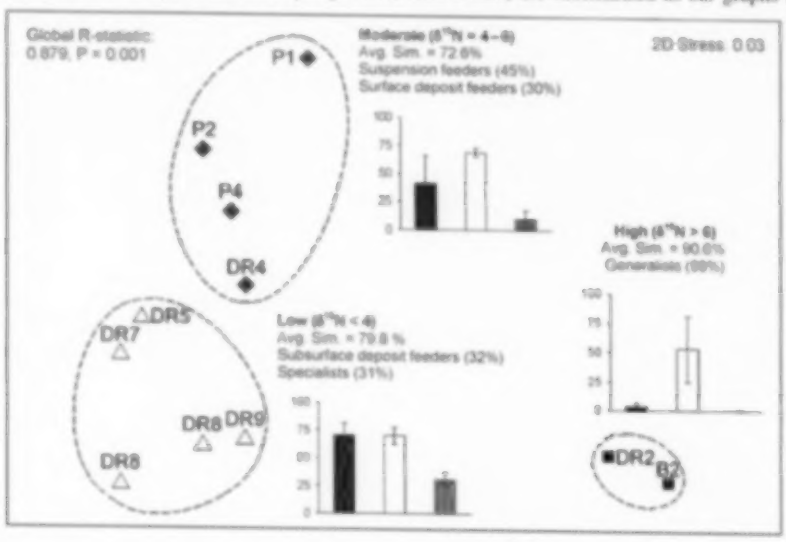
Fig. 5. Nonmetric multidimensional scaling (nMDS) ordination of mega-invertebrate consumer functional groups using square root transformed percent composition data (N = 11 sites). Low (open triangles, N = 5), moderate (shaded diamonds, N = 4), and high (solid squares, N = 2) levels of enrichment based on mean $\delta^{15}N$ values of *Pinna carnea* (*Lytechinus variegatus* for site B2). Broken line represents 67% average similarity contour based on hierarchical cluster analysis. Avg. Sim., average similarities within clusters, dominant consumer functional group(s), and percent contribution in parentheses. Mean (±1 standard error) biomass (g dry mass (DM)·m^{-2}) of seagrass resources (detritus, solid bars; *Thalassia*, open bars; and *Syringodium*, shaded bars) are summarized as bar graphs for each cluster.



Syringodium and macrodetritus by the increasing density of generalist consumers. However, at the highest levels of enrichment, *Thalassia*, the only remaining structure, also shows signs of reduction as long-term decreases in water quality (Vermeer 2000) and high generalist consumer density take their toll.

Discussion

Given the increasing levels of anthropogenic activities occurring in all ecosystems, it is prudent to begin examining similar systems across a gradient of such disturbances that may capture both subtle and dynamic thresholds of change that may be otherwise overlooked. Our analysis reveals that Caribbean seagrass communities become greatly simplified or homogenized with increased anthropogenic sources of nutrients and associated urbanization. Past theory and empirical evidence illustrates that declines in diversity lead to increasing simplification of ecological communities (McCann 2000). The patterns of increasing mega-invertebrate abundance (i.e., density) and decreasing diversity across the nutrient gradient are also in agreement with well-known empirical models (e.g., Pearson and Rosenberg 1978) of soft sediment communities. More broadly, the high consumer diversity and corresponding low consumer abundance at intermediate nutrient levels are consistent with the "intermediate disturbance hypothesis" (Connell 1978; Huston 1979). In this case, one must accept moderate levels of chronic nutrients as a disturbance facilitating low rates of competitive displacement and (or) periodic population reductions. Nonetheless, the distinct patterns of consumer abundance and diversity only partially describe the general dynamics of enrichment that have been observed in other studies (Weston 1990; Savage et al. 2002; Cardoso et al. 2004). In these seagrass systems, such patterns are accompanied by changes in the structure of the canopy, including a dramatic decrease in macrodetrital seagrass biomass and associated shifts in consumer functional groups. Although only a correlation, it strongly suggests that the three-dimensional structure created by the leaves and the decomposition dynamics of fallen leaves (i.e., detritus) play fundamental roles in the maintenance of consumer diversity and trophic structure by providing an exceptional combination of shelter and food resources (Ogden 1980; Hemminga and Duarte 2000).

It is reasonably well established that living seagrass tissue is not readily consumed by many consumers, although exceptions exist (Valentine and Heck 1999), and that the bulk of organic transfer in seagrass and some other aquatic systems to higher trophic levels is via the detrital pathway (Stoner et al. 1995; Wetzel 1995; Vizzini et al. 2002). The importance and preference of macrodetritus (Stoner and Waite 1991; Stoner et al. 1995) and particulate seagrass detritus (Harmelin et al. 1981) to a wide variety of primary consumers in seagrass communities substantiate the important link between diversity and detritus (Moore et al. 2004).

Although attempts to utilize trophic classifications in the analysis of environmental gradients have garnered mixed results (Weston 1990; Savage et al. 2002), the emerging patterns from this study suggest that distinct functional groups of primary consumers predominate at distinct ranges of anthropogenic nutrient enrichment. The relatively high diversity of mega-invertebrates, specifically specialists, at the low to moderate end of the nutrient enrichment spectrum is thought to be strongly linked to a diversity of resources ex-

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isting in the detrital pool (macrodetritus, particulate and resuspended forms, and the microbial, fungal, and metazoan community associated with decomposition) and sets the stage for the evolution and maintenance of detritivore diversity (Grall and Chauvaud 2002; Moore et al. 2004).

We hypothesize that high species diversity at the low to intermediate levels of nutrient enrichment depends on a number of features. Firstly, the primary producers (i.e., seagrass) that form the canopy and generate the majority of the detritus are well represented and of lower edibility (high lignin content) (Cebrian and Duarte 1998). This largely guarantees the existence of important shelter, substratum for attachment (e.g., epiphytes, eventually adding to detritus), and continued replenishment of a significant, donor-controlled, detrital pool. This in turn contributes to consumer diversity as the detrital pathway necessitates the involvement of a rich array of species and functional groups, the synergistic interactions of which lead to the physical and chemical breakdown of detritus (Moore et al. 2004). Finally, the relative densities of primary consumers, including those capable of direct producer consumption (i.e., regular urchins), are controlled through competition, predation, and intraguild predation, which prevents runaway consumption or dominance of any particular species or functional group (Polis et al. 1989; Polis and Strong 1996). The persistence of the seagrass detrital pool benefits many organisms, with detritus (and associated microbial, fungal, and metazoan film) serving as a nutritious food source, as well as shelter for many life history stages, including the extremely vulnerable postplanktonic larvae. It is perhaps then not surprising that with the loss of the seagrass detrital pool, we also see a significant loss of consumer diversity. The highest consumer diversity observed at intermediate levels of enrichment may be explained by a reduction in preferred habitat and food resources for dominate seagrass detritus–epiphyte specialists (i.e., conchs) (Stoner et al. 1995). At the same time, overall resource diversity increases through nutrient enrichment and associated pelagic production that facilitates a wider range of nonspecialist consumer functional groups that can coexist with reduced densities of specialists.

As nutrient enrichment begins to increase, all seagrasses may initially increase their productivity, including detrital production, with faster-growing, colonizing seagrasses (*Syringodium*) eventually being out competed by more competitive climax species (Williams 1990; Green and Webber 2003). The loss of *Syringodium* may begin to narrow the available resources within the traditional autochthonous pool. However, the potential emergence of macroalgae at intermediate nutrient enrichment may increase the resource pool, which may be a result of partial release from nutrient competition with seagrasses (Williams 1990). Increases in nutrients have also resulted in changes within the seagrass blade epiphyte community (McGlathery 1995). Continued input of nutrients may eventually initiate a switch to pelagic (i.e., phytoplankton) dominated production, which ultimately results in light limitations, sediment accretion, and decreased production of all benthic macrophytes (Grall and Chauvaud 2002; Green and Webber 2003; Vadeboncoeur et al. 2003). Although we were unable to measure pelagic production directly, our results are consistent with human-induced nutrient enrichment, as documented in a number of empirical studies in macrophyte systems (Grall and Chauvaud 2002; Green and Webber 2003; Vadeboncoeur et al. 2003).

The decrease in traditional benthic production, including a reduction of the canopy and associated macrodetritus, and the increased availability of phytoplankton and associated particulate detritus (i.e., phytodetritus) may allow the increase in surface deposit, suspension (both in a transitory manner), and relatively stable populations of generalist consumers. This is in light of declines in a number of consumer functional groups (i.e., specialists, subsurface deposit feeders) associated with relatively more pristine seagrass habitats that depend on seagrass detritus (Stoner and Waite 1991; Stoner et al. 1995; Tewfik et al. 2005). Consumers associated with pristine conditions (i.e., specialists, subsurface deposit feeders) may also significantly contribute to preventing runaway consumption of other species or functional groups, specifically generalist urchins, through competition (Tewfik 2005) and perhaps intraguild predation (Stoner and Waite 1991). Generalists are successively released over the nutrient gradient and allowed to increasingly erode the macrodetrital pool weakening the macrodetrital-dependent populations. Eventually, at the higher, chronic levels of nutrient enrichment, water quality may be severely impacted where even stress-tolerant or competitive producers (e.g., *Thalassia*), which facilitated the bulk of production, and consumers have difficulty maintaining themselves. Opportunistic generalists (e.g., urchins) may therefore switch to alternative resources (i.e., phytodetritus) that may be relatively abundant.

Phytodetritus can be a critical resource in both deep and shallow water benthic systems where assimilation by macrofauna contributes significantly to carbon flow and links to higher trophic levels (Levin et al. 1997; Iken et al. 2001; Moodley et al. 2005). The use of such alternate phytodetrital resources by generalist consumers (i.e., sea urchins) has been previously documented (Harmelin et al. 1981; Iken et al. 2001; Tewfik et al. 2005). Specifically, the contribution of particulate organic material (POM, including phytoplankton) to the sediment organic material (SOM) pool, determined using mixing models of $\delta^{13}C$ values of various resources, shifted from 7% to 44% between sites of low (DR6) and high (DR2) nutrient enrichment (Tewfik et al. 2005). Lower visibility and finer sediments (A. Tewfik, personal observation), as well as elevated amounts of SOM (approx. 2.8σ) per unit volume of sediment at the high nutrient-enriched site, lends additional support to increasing levels of POM (i.e., phytodetritus) settling to the benthos (Tewfik et al. 2005). Finally, enclosure experiments, using densities as high as 20 urchins·m^{-2}, indicated little use of either living *Thalassia* or its detritus at the high nutrient-enriched site (DR 2) as compared with intense grazing of these benthic resources at the low nutrient-enriched site (DR 6) (Tewfik 2005). Therefore, at the higher levels of nutrient enrichment, sea urchins may dominate because of the diminished community of macrodetritus-dependent competitors or intraguild predators and the availability of alternate resources combined with their overall morphological plasticity (Lawrence 1975; Harmelin et al. 1981).

In conclusion, Caribbean seagrass food webs impacted by increasing anthropogenic nutrient enrichment show substantial changes including loss of benthic resources (e.g., seagrass canopy, macrodetritus), overall reductions in benthic

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invertebrate consumer diversity, and a succession of dominant resources and consumer functional groups. Although a number of studies have illustrated the effects of anthropogenic nutrient enrichment on coastal systems (Weston 1990; McClelland and Valiela 1998; Cardoso et al. 2004), few have shown the progression of community change correlated with nutrient enrichment over such a broad range of sites as depicted here. This may have been facilitated by the examination of a clearly defined community of large, ubiquitous, mega-invertebrate consumers.

Here, we have begun to highlight some potentially powerful mechanisms operating within seagrass communities across a human-induced nutrient gradient. Our results highlight some future directions. Specifically, we hypothesize that the extremely high and relatively stable numbers of opportunistic generalist consumers (i.e., urchins) that mark our two most nutrient-enriched sites may be subsidized indirectly through high levels of nutrients. Such nutrients elevate the production of phytoplankton and associated detritus that are a well-known consequence of eutrophication (Duarte 1995; Cloern 2001; Vadeboncoeur et al. 2003). The high densities of urchins observed in the simplified communities may significantly restrain recovery of diversity as they consistently suppress both benthic macrophytes and competitive consumers through grazing and intraguild predation.

The importance of allochthonous subsidies has been documented via a number of different pathways in a variety of different systems: macroalgal detritus to desert islands (Polis et al. 1997) and submarine canyons (Vetter and Dayton 1999); phytoplankton detritus to abyssal plains (Iken et al. 2001); and fertilizers and agricultural production to waterfowl migration stopover sites (Jefferies 2000), often resulting in greatly increased numbers of generalist consumers that may ultimately depress in situ resources. Because of the allochthonous nature of these subsidies, such systems can remain stable even as complexity is lost and a single, large flow of energy dominates the system (Huxel and McCann 1998). We should expect that further declines in diversity will lead to accelerated simplification of natural systems (McCann 2000). Finally, although the overgrazing and deforestation of macrophyte-dominated systems has largely been attributed to predator and competition release of urchins as a result of overfishing, the contribution and potential significance of nutrient enrichment, as illustrated in our study, to the persistence of altered conditions should not be ignored.

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References

Adams, T., and Sterner, R. 2000. The effect of dietary nitrogen content on trophic level ^{15}N enrichment. Limnol. Oceanogr. **45**: 601–607.

Cabana, G., and Rasmussen, J.B. 1996. Comparison of aquatic food chains using nitrogen isotopes. Proc. Natl. Acad. Sci. U.S.A. **93**: 10 844 – 10 847.

Camp, D.K., Cobb, S.P., and van Breddveld, J.F. 1973. Overgrazing of grasses by a regular urchin, *Lytechinus variegatus*. Bioscience, **23**: 37–38.

Cardoso, P.G., Pardal, M.A., Lillebo, A.I., Ferreira, S.M., Raffaelli, D., and Marques, J.C. 2004. Dynamic changes in seagrass assemblages under eutrophication and implications for recovery. J Exp. Mar. Biol. Ecol. **302**: 233–248.

Carpenter, S., Ludwig, D., and Brock, W. 1999. Management of eutrophication for lakes subject to potentially irreversible change. Ecol. Appl. **9**: 751–771.

Cebrian, J., and Duarte, C.M. 1998. Patterns in leaf herbivory on seagrass. Aquat. Bot. **60**: 67–82.

Clarke, K.R., and Gorley, R.N. 2006. PRIMER v6: user manual/tutorial. PRIMER-E Ltd., Plymouth, UK.

Clarke, K.R., and Warwick, R.M. 2001. Change in marine communities, an approach to statistical analysis and interpretation. PRIMER-E Ltd., Plymouth, UK.

Cloern, J.E. 2001. Our evolving conceptual model of the coastal eutrophication problem. Mar. Ecol. Prog. Ser. **210**: 223–253.

Cole, M.L., Valiela, I., Kroeger, K.D., Tomasky, G.L., Cebrian, J., Wigand, C., McKinney, R.A., Grady, S.P., and da Silva, M.H.C. 2004. Assessment of a $\delta^{15}N$ isotopic method to indicate anthropogenic eutrophication in aquatic ecosystems. J. Environ. Qual. **33**(1): 124–132.

Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. Science (Washington, D.C.), **199**: 1302–1310.

DeAngelis, D. 1992. Dynamics of nutrient cycling and food webs. Chapman and Hall, London, UK.

Duarte, C.M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia, **41**: 87–112.

Duarte, C.M. 2002. The future of seagrass meadows. Environ. Conserv. **29**: 192–206.

Grall, J., and Chauvaud, L. 2002. Marine eutrophication and benthos: the need for new approaches and concepts. Global Change Biol. **8**: 813–830.

Green, S.O., and Webber, D.F. 2003. The effects of varying levels of eutrophication on phytoplankton and seagrass (*Thalassia testudinum*) populations of the southeast coast of Jamaica. Bull. Mar. Sci. **73**(2): 443–455.

Harmelin, J., Bouchon, C., and Hong, J. 1981. Impact de la pollution sur la distribution des echinodermes des substrats durs en provence (Mediterranee Nord-Occidentale). Tethys, **10**: 13–36.

Hemminga, M., and Duarte, C. 2000. Seagrass ecology. Cambridge University Press, Cambridge.

Hiscock, K. 1996. Marine nature conservation review: rationale and methods. Nature Conservancy Council, Peterborough, UK.

© 2007 NRC Canada

Hughes, T. 1994. Catastrophes, phase shifts, and large-scale degradation of Caribbean coral reefs. Science (Washington, D.C.), **265**: 1547–1551.

Huston, M. 1979. A general hypothesis of species diversity. Am. Nat. **113**: 81–101.

Hunel, G.R., and McCann, K.S. 1998. Food web stability: the influence of trophic flows across habitats. Am. Nat. **152**: 460–469.

Iken, K., Brey, T., Wand, U., Voigt, J., and Junghans, P. 2001. Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. Progr. Oceanogr. **50**: 383–405.

Jackson, D.A. 1997. Compositional data in community ecology: the paradigm or peril of proportions. Ecology, **78**: 929–940.

Jackson, J.B.C. 2001. What was natural in the coastal oceans? Proc. Natl. Acad. Sci. U.S.A. **98**: 5411–5418.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., B.J., B., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., and Warner, R.R. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science (Washington, D.C.), **293**: 629–638.

Jefferies, R. 2000. Allochthonous inputs: integrating population changes and food-web dynamics. Trends Ecol. Evol. **15**: 19–22.

Jefferies, R., Rockwell, R., and Abraham, K. 2004. Agricultural food subsidies, migratory conductivity and large-scale disturbance in arctic coastal systems: a case study. Integr. Comp. Biol. **44**: 130–139.

Lawrence, J. 1975. On the relationship between marine plants and sea urchins. Oceanogr. Mar. Biol: Annu. Rev. **13**: 213–286.

Levin, L., Blair, N., DeMaster, D., Plaia, G., Fornes, W., Martin, C., and Thomas, C. 1997. Rapid subduction of organic matter by maldanid polychaetes on the North Carolina slope. J. Mar. Res. **55**(3): 595–611.

Martinetto, P., Teichberg, M., and Valiela, I. 2006. Coupling of estuarine benthic and pelagic food webs to land-derived nitrogen sources in Waquoit Bay, Massachusetts, USA. Mar. Ecol. Prog. Ser. **307**: 37–48.

McCann, K.S. 2000. The diversity–stability debate. Nature (London), **405**: 228–233.

McCann, K.S. 2007. Protecting biostructure. Nature (London), **446**: 29.

McClelland, J.W., and Valiela, I. 1998. Changes in food web structure under the influence of increased anthropogenic nitrogen inputs to estuaries. Mar. Ecol. Prog. Ser. **168**: 259–271.

McClelland, J.W., Valiela, I., and Michener, R.H. 1997. Nitrogen-stable isotope signatures in estuarine food webs: a record of increasing urbanization in coastal watersheds. Limnol. Oceanogr. **42**: 930–937.

McGlathery, K.J. 1995. Nutrient and grazing influences on a subtropical seagrass community. Mar. Ecol. Prog. Ser. **122**: 239–252.

Minagawa, M., and Wada, E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochim. Cosmochim. Acta, **48**: 1135–1140.

Moodley, L., Middelburg, J.J., Soetaert, K., Boschker, H.T.S., Herman, P.M.J., and Heip, C.H.R. 2005. Similar rapid response to phytodetritus deposition in shallow and deep-sea sediments. J. Mar. Res. **63**(2): 457–469.

Moore, J., Berlow, E., Coleman, D., de Ruiter, P., Dong, Q., Hastings, A., Collins-Johnson, N., McCann, K., Melville, K., Morin, P., Nadelhoffer, K., Rosmond, A., Post, D., Sabo, J., Scow, K., Vanni, M., and Wall, D. 2004. Detritus, trophic dynamics, and biodiversity. Ecol. Lett. **7**: 584–600.

Ogden, J.C. 1980. Faunal relationships in Caribbean seagrass beds. *In* Handbook of seagrass biology: an ecosystem perspective. *Edited by* R. Phillips and C. McRoy. Garland STPM Press, New York. pp. 173–198.

Pearson, T., and Rosenberg, R. 1978. Macrobenthic successions in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. Annu. Rev. **16**: 229–311.

Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. **18**: 293–320.

Polis, G.A., and Strong, D.R. 1996. Food web complexity and community dynamics. Am. Nat. **147**: 813–846.

Polis, G.A., Myers, C.A., and Holt, R.D. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annu. Rev. Ecol. Syst. **20**: 297–330.

Polis, G.A., Anderson, W.B., and Holt, R.D. 1997. Toward an integration of landscape and food web ecology. Annu. Rev. Ecol. Syst. **28**: 289–316.

Rose, C.D., Sharp, W.C., Kenworthy, W.J., Hunt, J.H., Lyons, W., G., Prager, E.J., Valentine, J.F., Hall, M.O., Whitfield, P.E., and Fourqurean, J.W. 1999. Overgrazing of a large seagrass bed by the sea urchin *Lytechinus variegatus* in Outer Florida Bay. Mar. Ecol. Prog. Ser. **190**: 211–222.

Savage, C., Elmgren, R., and Larsson, U. 2002. Effects of sewage derived nutrients on an esturine macrobenthic community. Mar. Ecol. Prog. Ser. **243**: 67–82.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., and Walker, B. 2001. Catastrophic shifts in ecosystems. Nature (London), **413**: 591–596.

Short, F.T., and Wyllie-Echeverria, S. 1996. Natural and human-induced disturbance of seagrasses. Environ. Conserv. **23**: 17–27.

Stoner, A.W., and Waite, J.M. 1991. Trophic biology of *Strombus gigas* in nursery habitats: diets and food sources in seagrass meadows. J. Moll. Stud. **57**: 451–460.

Stoner, A.W., Ray, M., and Waite, J.M. 1995. Effects of a large herbivorous gastropod on macrofauna communities in tropical seagrass meadows. Mar. Ecol. Prog. Ser. **121**: 125–137.

SYSTAT. 2001. SigmaPlot 2001 for windows. SYSTAT Software Inc., Richmond, California.

Tewfik, A. 2005. Patterns and effects of disturbance in Caribbean macrophyte communities. Ph.D. dissertation, Department of Biology, McGill University, Montreal, Quebec.

Tewfik, A., Rasmussen, J.B., and McCann, K.S. 2005. Anthropogenic enrichment alters a marine benthic food web. Ecology, **86**(10): 2726–2736.

Vadeboncoeur, Y., Jeppesen, E., Vander Zanden, M.J., Schierup, H.H., Christoffersen, K., and Lodge, D.M. 2003. From Greenland to green lakes: cultural eutrophication and the loss of the benthic pathways in lakes. Limnol. Oceanogr. **48**: 1408–1418.

Valentine, J.F., and Heck, K.L. 1991. The role of sea urchin herbivory in regulating subtropical seagrass meadows: evidence from field manipulations in the Northern Gulf of Mexico. J. Exp. Mar. Biol. Ecol. **154**: 215–230.

Valentine, J.F., and Heck, K.L. 1999. Seagrass herbivory: evidence for continued grazing of marine grasses. Mar. Ecol. Prog. Ser. **176**: 291–302.

Vanderklift, M.A., and Ponsard, S. 2003. Sources of variation in consumer-diet $\delta^{15}N$ enrichment: a meta-analysis. Oecologia, **136**: 169–182.

Vermeer, L. 2000. Changes in growth and abundance of seagrass in Barbados. Ph.D. thesis, Department of Biology, Dalhousie University, Halifax, Nova Scotia.

Vetter, E., and Dayton, P. 1999. Organic enrichment by macrophyte detritus and abundance patterns of megafaunal populations in submarine canyons. Mar. Ecol. Prog. Ser. **186**: 137–148.

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Vizzini, S., Sara, G., Michener, R.H., and Mazzola, A. 2002. The role and contribution of seagrass *Posidonia oceanica* (L.) Delile organic matter for secondary consumers as revealed by carbon and nitrogen stable isotope analysis. Acta Oecol. **23**: 277–285.

Weston, D.P. 1990. Quanitative examination of macrobenthic community changes along an organic enrichment gradient. Mar. Ecol. Prog. Ser. **61**: 233–244.

Wetzel, R.G. 1995. Death, detritus, and energy flow in aquatic ecosystems. Freshw. Biol. **33**: 83–89.

Williams, S.L. 1990. Experimental studies of Caribbean seagrass bed development. Ecol. Monogr. **60**: 449–469.

Zar, J.H. 1999. Biostatistical analysis. Prentice-Hall, Inc., London, UK.

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Regional trends in fish mean length at age: components of variance and the statistical power to detect trends

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Abstract: We examined statewide time series (1940s–2002) of mean length at ages 2, 3, and 4 for seven fish species sampled from Michigan and Wisconsin inland lakes for temporal trends. We used a components of variance approach to examine how total variation in mean length at age was partitioned into lake-to-lake, coherent temporal, ephemeral temporal, trend, and residual variation. Using these estimated variance components, we simulated the effects of different variance structures on the power to detect trends in mean length at age. Of the 42 data sets examined, only four demonstrated significant regional (statewide) trends: age 4 largemouth bass (*Micropterus salmoides*) from Wisconsin lakes increased about 0.7 mm·year^{-1} in mean length at age, and ages 2, 3, and 4 walleye (*Sander vitreus*) from Wisconsin lakes decreased between 0.5 and 0.9 mm·year^{-1} in mean length at age. The structure of variation differed substantially among data sets, and these differences strongly affected the power to detect trends. Of particular note was that even modest levels of coherent temporal variation led to substantial decreases in power for detecting trends. To maximize trend detection capabilities, fisheries management agencies should consider variance structures prior to choosing indices for monitoring and realize that trend detection capabilities are species- and region-specific.

Résumé : Afin de déceler des tendances temporelles, nous avons examiné des séries chronologiques (années 1940 à 2002) de longueurs moyennes aux âges 2, 3 et 4 de sept espèces de poissons échantillonnés dans les lacs intérieurs sur l'ensemble du territoire des états du Michigan et du Wisconsin. Nous avons utilisé la méthode des composantes de la variance pour déterminer de quelle manière la variation totale des longueurs moyennes en fonction de l'âge peut se répartir en diverses composantes, soit en variation entre les lacs, en variations temporelles cohérente et éphémère, en variation reliée aux tendances et en variation résiduelle. À l'aide de ces composantes estimées de la variance, nous avons simulé les effets de diverses structures de la variance sur la puissance de détection des tendances dans les longueurs moyennes en fonction de l'âge. Des 42 séries de données examinées, seules quatre montrent des tendances régionales (à l'échelle de l'état) significatives: les achigans à grande bouche (*Micropterus salmoides*) d'âge 4 des lacs du Wisconsin ont augmenté d'environ 0,7 mm·année^{-1} en longueur moyenne en fonction de l'âge, alors que les dorés jaune (*Sander vitreus*) d'âges 2, 3 et 4 des lacs du Wisconsin ont diminué de 0,5 à 0,9 mm·année^{-1} en longueur moyenne en fonction de l'âge. La structure de la variation diffère considérablement entre les banques de données et ces différences affectent fortement la puissance de détection des tendances. En particulier, même des niveaux modestes de variation temporelle cohérente font diminuer considérablement la puissance de détection des tendances. Afin de maximiser leurs capacités de détection des tendances, les agences de gestion des pêches devraient examiner les structures de variance avant de choisir des indices de surveillance; elles devraient aussi se rendre compte que les capacités de détection des tendances varient de façon spécifique en fonction des espèces et des régions.

[Traduit par la Rédaction]

Introduction

Knowledge of trends in fish growth rates is important ecologically, as growth rates influence ecological interactions and population dynamics and are often used along with recruitment and mortality information to assist management decisions (Trippel 1993). Furthermore, growth rates are influenced by environmental conditions and can represent an integrative measure of conditions experienced by a fish over its lifetime. Consequently, one goal of many fishery monitoring programs is to determine whether growth of fish populations (e.g., as indicated by mean size at age) is changing

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with time and if so, whether such changes are consistent across species and across systems.

Factors that lead to changes in fish growth over time and space include both biotic factors such as differences in prey abundance and fish density (i.e., density-dependent growth; Claramunt and Wahl 2000; Quist et al. 2003; Sass et al. 2004) and abiotic factors such as differences in water temperature and lake morphometry characteristics (e.g., lake area; Claramunt and Wahl 2000; Quist et al. 2003). Many of these factors change temporally (e.g., yearly variation in temperature and regional management plans) and may lead to regional temporal trends in growth rates. Others vary spatially; for example, density-dependent growth of walleye in northern Wisconsin was shown to be density dependent within individual lakes; however, it was noted that the degree of density dependence among lakes differed spatially likely because of lake-specific properties, such as differences in productivity, prey species composition and abundance, and management regime (Sass et al. 2004).

Most work on evaluating trends in fish growth has focused on individual populations (e.g., Reckahn 1986; Szalai et al. 2003; He and Bence 2007). Although, there have been some regional evaluations of trends in fish demographics (McDonough and Buchanan 1991; Beard and Kampa 1999; Grant et al. 2004), the majority of aquatic work evaluating trends has emphasized single systems and water quality across rivers (Antonopoulos et al. 2001), lakes (Jassby et al. 1999, but see Urquhart et al. 1998 and Larsen et al. 1995), and seas (Sandén and Håkansson 1996). Although investigations into temporal trends within individual systems provide valuable information, the ability to detect regional (e.g., statewide) temporal trends is crucial for the evaluation of many management actions and to examine responses to natural or anthropogenic perturbations. Furthermore, the early detection of regional changes is important in many cases to allow time for managers and policy-makers to respond and take appropriate action (Vaughan et al. 2001). This said, detection of regional trends in fish growth (or other parameters) is challenging because available data are often limited, and regional trends can become obscured by large amounts of temporal variation common to the region or unique to particular populations within a region.

We provide one approach to evaluating regional trends in fish growth and use the estimated structures of variance to evaluate the statistical power of different sampling designs for detecting regional trends in fish growth. Mean size at age data are the most frequently available information on fish growth and provide an integrative measure of fish growth over the fish lifespan up to the age it was collected. In the data sets we considered, the same lake was only infrequently sampled in two sequential years, and data were commonly missing for one or more ages. Consequently, we analyzed mean size at age separately for each age as an index of growth. We use these results to provide insight into design and feasibility of reliable monitoring programs.

Trends and components of variance

A components of variance approach has been advocated to address the issue of variability in ecological data when evaluating regional temporal trends and monitoring of ecological systems (Urquhart et al. 1998; Larsen et al. 2001; Kincaid et al. 2004). Under this framework, total variance is partitioned into four components, including (*i*) site-to-site (spatial) variation, (*ii*) coherent (year-to-year) variation affecting all sites (e.g., lakes) in a similar manner, (*iii*) ephemeral temporal variation (e.g., site × year interaction) corresponding to independent yearly variation at each site, and (*iv*) residual variation (Larsen et al. 2001; Kincaid et al. 2004). A fifth component can be included in this framework in which each site has its own trend (i.e., trend variation: allowing the slope of the response variable versus time at each site to be a draw from a distribution and estimate the variance of the distribution of slopes; VanLeeuwen et al. 1996).

Although the total variance of the data is one of the primary factors affecting the ability to detect trends (Stow et al. 1998), the structure of that variance is far more important; likewise the temporal sampling design can be more important than total variation. Power analysis is a useful tool for evaluating the performance of ecological monitoring programs (Peterman 1990; Fairweather 1991; Hatch 2003) and in particular for investigating how specific variance components affect the power to detect trends for a given sampling design. Ideally, a monitoring program should have high statistical power, or the ability to detect a specific deviation from a null hypothesis.

Random effects models have been used to partition variability in fish growth data (e.g., changes in annual increment in length, Osenberg et al. 1988). However, to our knowledge, a components of variance approach has not been applied to mean length at age or other fish growth data within the context of trend detection over a large spatial region, even though fisheries agencies are collecting length at age data through time to monitor regions of lakes and streams (e.g., Hayes et al. 2003). The specific objectives of this study were to (*i*) determine if trends are evident in mean length at age for seven fish species in Michigan and Wisconsin inland lakes, (*ii*) quantify the components of variance for mean length at age, and (*iii*) perform power analyses to investigate the effects of the different components of variance on the statistical power to detect trends and to evaluate alternative sampling designs.

Materials and methods

Data sets

We obtained mean length at age data for seven fish species collected during survey sampling of inland lakes conducted by the Fisheries Division of the Michigan Department of Natural Resources (MIDNR) and the Wisconsin Department of Natural Resources. We included bluegill (*Lepomis macrochirus*), pumpkinseed (*Lepomis gibbosus*), largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), yellow perch (*Perca flavescens*), walleye (*Sander vitreus*), and northern pike (*Esox lucius*) because of their prevalence in the historical data. In each lake survey, length at age was measured; mean length at age is available in the long-term data set by species and age. The corresponding number of fish that contributed to the mean was also recorded along with the day of year that sampling occurred. We restricted our analyses to mean length at ages 2, 3, and 4 for each species because the reliability of fish

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Table 1. Fish species, age, sample size (*N*, number of observations used in the analyses), gear type used to collect fish, and sampling years used in the trend analysis for Michigan and Wisconsin inland lakes.

	N		Gear type		Sampling years	
Species (age)	Michigan	Wisconsin	Michigan	Wisconsin	Michigan	Wisconsin
BLG (2)	261	162	Electrofisher	Electrofisher	1961–2002	1959–2003
BLG (3)	265	216	Electrofisher	Electrofisher	1962–2002	1958–2003
BLG (4)	261	245	Electrofisher	Electrofisher	1963–2002	1958–2003
PSF (2)	51	66	Trap net	Electrofisher	1960–2002	1959–2003
PSF (3)	120	132	Trap net	Electrofisher	1960–2003	1959–1992
PSF (4)	143	146	Trap net	Electrofisher	1958–2003	1959–1992
LMB (2)	277	227	Electrofisher	Electrofisher	1961–2002	1958–2003
LMB (3)	275	285	Electrofisher	Electrofisher	1963–2002	1959–2003
LMB (4)	243	273	Electrofisher	Electrofisher	1963–2002	1959–2002
SMB (2)	93	52	Electrofisher	Electrofisher	1963–2001	1957–2003
SMB (3)	74	47	Electrofisher	Electrofisher	1963–2001	1957–2003
SMB (4)	61	44	Electrofisher	Electrofisher	1963–1999	1956–2003
YEP (2)	266	167	Electrofisher	Electrofisher	1961–2002	1958–2003
YEP (3)	229	203	Electrofisher	Electrofisher	1961–2002	1958–2003
YEP (4)	185	187	Electrofisher	Electrofisher	1961–2002	1958–2003
NOP (2)	157	166	Fyke net	Fyke net	1960–2002	1947–2002
NOP (3)	161	176	Fyke net	Fyke net	1957–2002	1947–2002
NOP (4)	151	183	Fyke net	Fyke net	1957–2002	1947–2002
WAE (2)	236	303	Electrofisher	Fyke net	1967–2002	1946–2001
WAE (3)	210	401	Electrofisher	Fyke net	1967–2002	1946–2001
WAE (4)	176	434	Electrofisher	Fyke net	1967–2002	1946–2001

Note: BLG, bluegill (*Lepomis macrochirus*); PSF, pumpkinseed (*Lepomis gibbosus*); LMB, largemouth bass (*Micropterus salmoides*); SMB, smallmouth bass (*Micropterus dolomieu*); YEP, yellow perch (*Perca flavescens*); NOP, northern pike (*Esox lucius*); WAE, walleye (*Sander vitreus*).

ageing decreases with increasing age (Ricker 1975) and because these ages had adequate sample sizes.

Mean length at age time series were available beginning in the early 1960s and continuing to the early 2000s for fish collected in Michigan and from the late 1940s or late 1950s to the early 2000s for fish collected in Wisconsin (Table 1). Fish were collected using a variety of gear types over the time series. Thus, in an effort to reduce potential biases introduced by using different sampling gear, we only retained fish collected using the same gear type in the analyses for each species, age, and state combination (Table 1). For nets, however, (e.g., trap nets and fyke nets) the mesh size was not recorded over time; thus we could not control for any potential changes in mesh size. Historically, fish were not sampled in a truly random design by the state agencies. However, the fish growth surveys used in this analysis represent a large sample of public lakes broadly distributed throughout both states, thus reducing the likelihood of substantial bias.

Temporal trend statistical analysis

A mixed model was used to assess the presence of regional (statewide) linear trends in mean length at age for each species, similar to that suggested by Piepho and Ogutu (2002). Although we restricted our analysis to the investigation of linear trends, if a monotonic increase or decrease is present, then a linear trend will be present (Urquhart and Kincaid 1999). Each state and species–age data set was analyzed separately because differences in sampling methodologies between agencies could influence variance components and possibly the overall trends. Each data point (mean length at age) was weighted by the number of fish that contributed to each mean for each lake. To account for potential variation introduced by fish being sampled during different times of the year (i.e., seasonal trends in mean length at age), seasonal trends were examined prior to the interannual analysis by fitting linear and quadratic least-squares regression models (Grant et al. 2004). For each species–age combination with a significant seasonal trend, the regression equation was used to adjust mean length at age to the median sample date.

The mixed model used for the analyses was

$$(1) \qquad Y_{ij} = \mu + a_i + y(\lambda + t_i) + b_j + c_{ij} + e_{ij}$$

where Y_{ij} is the mean length at age for lake i in year j, and μ and λ are the fixed intercept and slope (fixed regional trend), respectively. The random effect a_i is a random effect for lake i, representing lake-to-lake variability, independent and identically distributed (iid) as $N(0, \sigma_a^2)$; b_j is a random effect for the jth year (coherent temporal variability), iid as $N(0, \sigma_b^2)$; t_i is a random effect for the trend for lake i, iid as $N(0, \sigma_t^2)$; c_{ij} is the lake × year interaction (ephemeral temporal variability), iid as $N(0, \sigma_c^2)$; and e_{ij} is the unexplained error (residual error), independent as $N(0, \sigma_e^2/n_{ij})$. Note that e_{ij} represents sampling error that influences the observed mean length at age, and this variance is assumed to be inversely related to sample size (n_{ij}). In practice, this means that the model was fit by weighting observations (means for a year and age) by their sample sizes, and σ_e^2 should be viewed as describing variation among individual fish. The year covariate (y) is the

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*j*th year minus the mean year used in the analysis. This standardization of year was performed to provide numerical stability.

We estimated variance components using restricted maximum likelihood and *P* values using a likelihood ratio test (Self and Liang 1987; Littell et al. 1996). We considered all analyses significant at $P < 0.05$. Because we could not estimate the lake × year interaction effect for most data sets (e.g., the data sets did not contain sufficient data on lakes sampled multiple times within a year or overall sample size was small), we used a simpler model to examine temporal trends that excludes the estimation of the variance due to lake × year interaction. In this case, the variance due to the lake × year interaction is contained within the residual error term. Not estimating this parameter, however, does not affect the estimate of the slope.

Power analysis

We investigated the extent to which the following factors affected the ability to detect a trend: (1) increasing trend magnitude (λ ranged from –0.5 to 2.0 mm·year^{-1}), (2) increasing number of fish sampled per lake (ranging from 5 to 30 fish·lake^{-1}), (3) increasing the number of lakes sampled per year (ranging from 10 to 40 lakes·year^{-1}), (4) decreasing lake effect variance, and (5) sampling from a population of 50 or 1000 lakes. We address factor 1 to provide information on the effects of trend magnitude on power; factors 2 and 3 are addressed because the number of fish and lakes sampled is an important consideration for sampling designs with respect to allocating personnel and fiscal time and money resources. We address factor 4 to understand how power would increase if lake-to-lake variance was reduced, for example, by using a lake classification scheme. To this end, we reduced lake-to-lake variance by 50% and then reduced it to zero to explore the effects of a large reduction in lake-to-lake variance. Finally, we examined factor 5 to examine how the proportion of lakes sampled each year influences statistical power. For simulations for which sampling from a population of 50 or 1000 lakes did not change the general patterns observed, we report only those results for sampling from a 50-lake population, unless otherwise stated.

We used a simulation approach to examine the statistical power to detect temporal trends using the variance components estimated from eq. 1. For each simulation, 1000 data sets were generated containing species-specific mean length at age data for a population of lakes (50 or 1000 lakes; see below) over 25 years. First, a true mean length at age for each lake in the population was generated over the 25-year time period. A trend of known magnitude (e.g., a decease of 1 mm·year^{-1}) was also incorporated into the data set. Using the true mean lengths at ages for each lake, an observed mean length at age was then generated for each lake by randomly generating lengths for a prespecified number of fish (ranging from 5 to 30) for each of the lakes from a normal distribution with a mean equal to the true mean and variance equal to the estimated residual (sampling) variance from eq. 1. From these 1000 data sets, a user-specified number of lakes (ranging from 10 to 40) were then randomly sampled from the population of 50 or 1000 lakes each year. When the number of fish sampled per lake was held constant, we used the mean number of fish sampled per age class from our surveys ($\bar{x} = 10$). Thirty lakes sampled per year was used as a realistic number of lakes that could be sampled per year by a management agency when the number of lakes sampled per year was held constant (K. Wehrly, Fisheries Division, MIDNR, Institute of Fisheries Research, 1109 North University Avenue, Ann Arbor, MI 48109, USA, personal communication). Lakes were sampled without replacement within a year, but all lakes were available for selection each year. Data were analyzed for different sampling durations from 5 up to 25 years and analyzed for the presence of a trend. The model specified in eq. 1 was used to test the null hypothesis that $\hat{\lambda} = 0$ for each data set, and the test statistic was calculated and compared with a critical value ($\alpha = 0.05$). Because the data generated depict a situation in which we know the null hypothesis is false (i.e., a trend of known magnitude was incorporated into the data), power was estimated as the percentage of trials (out of 1000) that rejected the null hypothesis.

Results

Temporal trend

Not all data sets contained enough information to fit the model to evaluate temporal trends. Of 42 data sets examined (7 species × 3 ages × 2 states), we were able to examine temporal trends for only 26 data sets (Table 2). Of the 26 analyses, only four demonstrated significant temporal trends. The slope estimate for age 4 largemouth bass from Wisconsin lakes was significant, with an increase of about 0.7 mm·year^{-1} in mean length at age. Ages 2, 3, and 4 walleye from Wisconsin lakes showed a negative trend, decreasing between 0.5 and 0.9 mm·year^{-1} in mean length at age (Table 2). For all other analyses, estimates of the slope for the fixed regional trend had absolute values of 0.43 mm·year^{-1} or less, which were not significantly different from zero at our specified alpha level ($P > 0.05$).

Variance components

We could not estimate the lake × year interaction effect for 20 of 26 of the data sets used in trend estimation. For the data sets where estimation was possible, the structure of variation differed substantially among data sets (Table 3; Fig. 1). Mean residual variation $\hat{\sigma}^2_\varepsilon$ was 54% and ranged from 18.1% to 75.7% of the total variation. Mean ephemeral temporal variation ($\hat{\sigma}^2_\tau$) was 17.2% and ranged from 4.9% to 30.6% of the total variation. The mean percentage of total variation attributed to coherent temporal variation $\hat{\sigma}^2_\zeta$ was 3.5% and ranged from 0.5% to 8.7%. The mean percentage of total variation attributed to lake-to-lake differences $\hat{\sigma}^2_\alpha$ was 25.4% and ranged from 5.5% to 50.5%. The mean percentage of the total variation due to trend variation $\hat{\sigma}^2_t$ was small (mean = 0.1%), ranging from 0.01% to 0.24%.

Power analysis

We investigated the effects of variance structures on statistical power by contrasting two carefully chosen data sets, which had strikingly different variance structures, namely age 4 walleye sampled in Michigan and Wisconsin (Fig. 1). Because the slope estimates for the significant analyses of temporal trends ranged from –0.5 to –0.9, we used $\lambda = -1.0$ mm·year^{-1} for simulations in

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Table 2. Parameter estimates for the fixed effect of sampling year (fixed regional trend (mm·year^{-1}), $\hat{\lambda}$) followed by standard error (SE) in parentheses, F value, and P value for mean length at age of seven fish species in Michigan and Wisconsin inland lakes.

	$\hat{\lambda}$ (SE)		F		P	
Species (age)	Michigan	Wisconsin	Michigan	Wisconsin	Michigan	Wisconsin
BLG (2)	–0.176 (0.160)	NE	1.20	NE	0.282	NE
BLG (3)	–0.012 (0.173)	–0.425 (0.195)	0.01	4.73	0.944	0.118
BLG (4)	0.004 (0.198)	–0.413 (0.196)	0.00	4.43	0.983	0.059
PSF (2)	NE	NE	NE	NE	NE	NE
PSF (3)	–0.046 (0.262)	NE	0.03	NE	0.873	NE
PSF (4)	0.066 (0.237)	–0.381 (0.242)	0.08	2.48	0.788	0.176
LMB (2)	–0.221 (0.265)	NE	0.69	NE	0.412	NE
LMB (3)	–0.390 (0.267)	0.306 (0.314)	2.13	0.95	0.157	0.338
LMB (4)	–0.292 (0.285)	**0.672 (0.313)**	1.05	**4.59**	0.326	**0.045**
SMB (2)	–0.202 (0.425)	NE	0.23	NE	0.655	NE
SMB (3)	–0.392 (0.743)	NE	0.28	NE	0.626	NE
SMB (4)	NE	NE	NE	NE	NE	NE
YEP (2)	–0.077 (0.176)	NE	0.19	NE	0.665	NE
YEP (3)	–0.271 (0.210)	NE	1.69	NE	0.213	NE
YEP (4)	0.165 (0.260)	NE	0.40	NE	0.545	NE
NOP (2)	–0.430 (0.753)	NE	0.33	NE	0.577	NE
NOP (3)	NE	NE	NE	NE	NE	NE
NOP (4)	NE	–0.036 (0.435)	NE	0.01	NE	0.947
WAE (2)	0.096 (0.448)	**–0.917 (0.283)**	0.05	**10.52**	0.831	**0.002**
WAE (3)	0.074 (0.918)	**–0.530 (0.257)**	0.01	**4.26**	0.936	**0.042**
WAE (4)	0.138 (0.816)	**–0.676 (0.237)**	0.03	**8.13**	0.867	**0.005**

Note: Significant regional trends are shown in bold ($\alpha = 0.05$). BLG, bluegill (*Lepomis macrochirus*); PSF, pumpkinseed (*Lepomis gibbosus*); LMB, largemouth bass (*Micropterus salmoides*); SMB, smallmouth bass (*Micropterus dolomieu*); YEP, yellow perch (*Perca flavescens*); NOP, northern pike (*Esox lucius*); WAE, walleye (*Sander vitreus*); NE, not estimable.

Table 3. Estimated variance components followed by standard error in parentheses from a weighted mixed model examining mean length at age over time for Michigan and Wisconsin inland lakes.

Species (age)	Lake-to-lake ($\hat{\sigma}^2_L$)	Coherent temporal ($\hat{\sigma}^2_C$)	Ephemeral temporal ($\hat{\sigma}^2_E$)	Trend variation ($\hat{\sigma}^2_T$)	Residual error ($\hat{\sigma}^2_\varepsilon$)
Michigan					
YEP (2)	59.1 (91.4)	**31.6 (23.5)**	**227.1 (100.4)**	0.4 (0.43)	**765.9 (200.4)**
LMB (3)	**240.9 (108.8)**	32.8 (40.1)	**455.4 (121.4)**	1.4 (1.1)	**1145.0 (261.0)**
WAE (3)	**1526.4 (368.8)**	95.5 (101.6)	**533.7 (168.8)**	**8.2 (4.7)**	**1238.8 (315.4)**
WAE (4)	**1531.8 (402.0)**	16.1 (88.4)	**928.4 (268.2)**	4.9 (4.2)	**549.9 (216.1)**
Wisconsin					
WAE (3)	**833.5 (139.9)**	**313.2 (179.1)**	**225.6 (63.9)**	0.4 (0.4)	**2230.9 (504.9)**
WAE (4)	**1001.8 (167.6)**	**260.7 (155.6)**	**319.3 (87.9)**	**0.8 (0.5)**	**4936.2 (1063.9)**

Note: Variance components significantly different from zero are shown in bold ($\alpha = 0.05$). YEP, yellow perch (*Perca flavescens*); LMB, largemouth bass (*Micropterus salmoides*); WAE, walleye (*Sander vitreus*).

which λ was held constant. Trends less than this would likely not be considered biologically significant in the short term.

The power to detect trends in mean length at age increased, as expected, with increasing trend magnitude (Fig. 2). For example, after 15 years of sampling, the power to detect a trend increased from 0.2 to 1.0 as λ decreased from –0.5 to –2.0 mm·year^{-1} for age 4 walleye sampled from Michigan lakes. For age 4 walleye sampled from Wisconsin lakes, power also increased with trend magnitude, but power at a given number of years and trend magnitude was markedly lower in Wisconsin as compared with Michigan, demonstrating the influence of the different variance structures between states.

In an effort to visualize the trade-offs between sampling more fish per lake versus sampling more lakes per year, we plotted power curves for both Michigan and Wisconsin walleye across 10- and 25-year sampling periods (Fig. 3). For walleye sampled in Michigan, the greatest increase in power at 10 years of sampling was gained by increasing the number of lakes sampled each year, with only a slight gain in power achieved by increasing the number of fish sampled in each lake. For example, if 30 lakes were sampled per year, increasing the number of fish sampled from 5 to 30 increased power by only 0.05. In contrast, assuming 10 fish were sampled from each lake, increasing the number of lakes sampled from 10 to 40 increased power by 0.3. A similar pattern was observed at 25 years; however, relatively high power (ranging from 0.85 to 1.0) was obtained regardless of the number of lakes or fish sampled (Fig. 3).

A different pattern was observed for walleye sampled from Wisconsin (Fig. 3). At 10 and 25 years of sampling, al-

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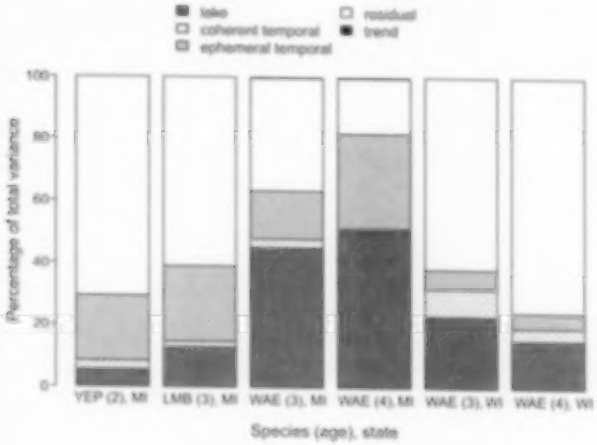
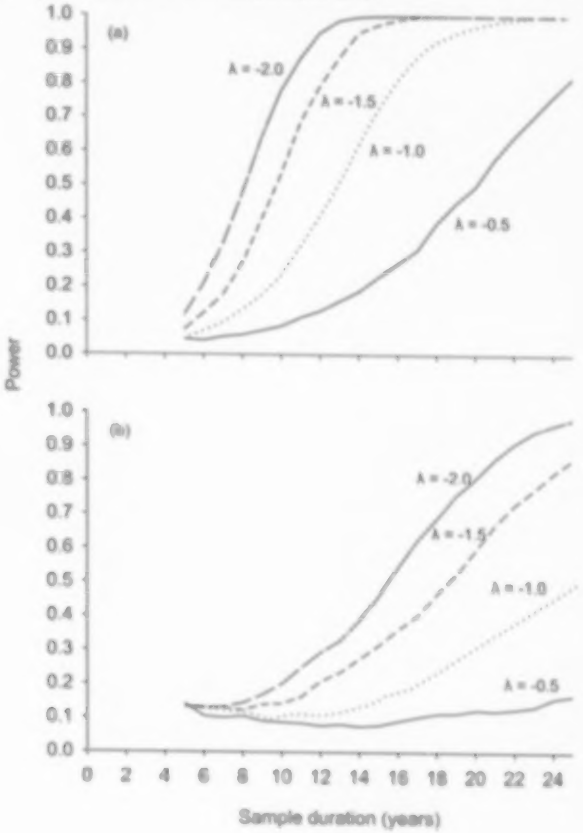
Fig. 1. Estimated percentage of total variation attributed to lake, coherent temporal, ephemeral temporal, trend variation, and residual variance. Estimates are from a mixed model for mean length at age versus time for six species–age combinations of fish from Michigan (MI) and Wisconsin (WI) inland lakes. YEP, yellow perch (*Perca flavescens*); LMB, largemouth bass (*Micropterus salmoides*); WAE, walleye (*Sander vitreus*). Note that trend variation is a very small percentage of the total variation and is only visible at the top of the bars for age 3 and 4 walleye from Michigan.



though increasing the number of lakes sampled each year from 10 to 20 increased power, power leveled off and remained relatively low even as the number of lakes increased from 20 to 40. Increasing the number of fish sampled from each lake did increase power; however, this increase was quite small. These patterns reflect the influence on the larger coherent temporal variance component in the Wisconsin data set.

Decreasing lake-to-lake variance did not have a noticeable effect on power for either walleye sampled in Michigan or Wisconsin when 60% of the total population of lakes was sampled each year (sampling 30 out of 50 lakes each year). The 60% sampling rate led to many revisits, thus letting the statistical analysis estimate and remove the lake effect from the trend detection. Power remained similar at all sampling durations (Fig. 4), but was consistently higher for Michigan compared with Wisconsin lakes, again reflecting the larger coherent temporal variance in the Wisconsin analysis. Under the scenario in which 3% of the lakes were sampled each year (sampling 30 out of 1000 lakes each year), decreasing lake-to-lake variance resulted in an increase in power for walleye sampled in Michigan, where lake-to-lake variance composed 51% of the total variance; however, this pattern of increasing power with decreasing lake-to-lake variance was not observed with the walleye sampled in Wisconsin lakes, where lake-to-lake variance was smaller, composing 15% of the total variance (Fig. 4). Furthermore, when sampling a small percentage (e.g., 3%) of the population of lakes, some models were not estimable over short sampling durations (<10 years) because there were not sufficient data on individual lakes sampled repeatedly over time. Thus, power estimates reported for sampling from the 1000 lake scenario are

Fig. 2. Power curves for detecting temporal trends in mean length at age with increasing trend magnitude (λ = mm·year^{-1}) for age 4 walleye (*Sander vitreus*) in Michigan (*a*) and Wisconsin (*b*) inland lakes (30 lakes sampled each year out of a population of 50 lakes, 10 fish sampled per lake).



only for models that were estimable (i.e., the number of trials was <1000).

Discussion

Temporal trend

We detected four significant regional trends out of the 26 data sets analyzed, all of which were from inland lakes sampled in Wisconsin. Of these, one was positive (age 4 largemouth bass) and three were negative (ages 2, 3, and 4 walleye). The magnitude of the trends ranged from 0.5 to 0.9 mm·year^{-1}. No significant regional trends in mean length at age were detected from Michigan inland lakes. Although we detected four significant regional trends, any inference regarding causation is difficult (Stow et al. 1998); however, potential mechanisms can be hypothesized. For instance, potential causal factors of increasing trends in mean length at age include effective regional harvest regulations or increases in regional temperatures resulting in increased growth rates. However, if increases in regional temperature were responsible for the observed increasing trend, then we would expect that more of our data sets would demonstrate such a trend. Thus, temperature alone is likely not responsi-

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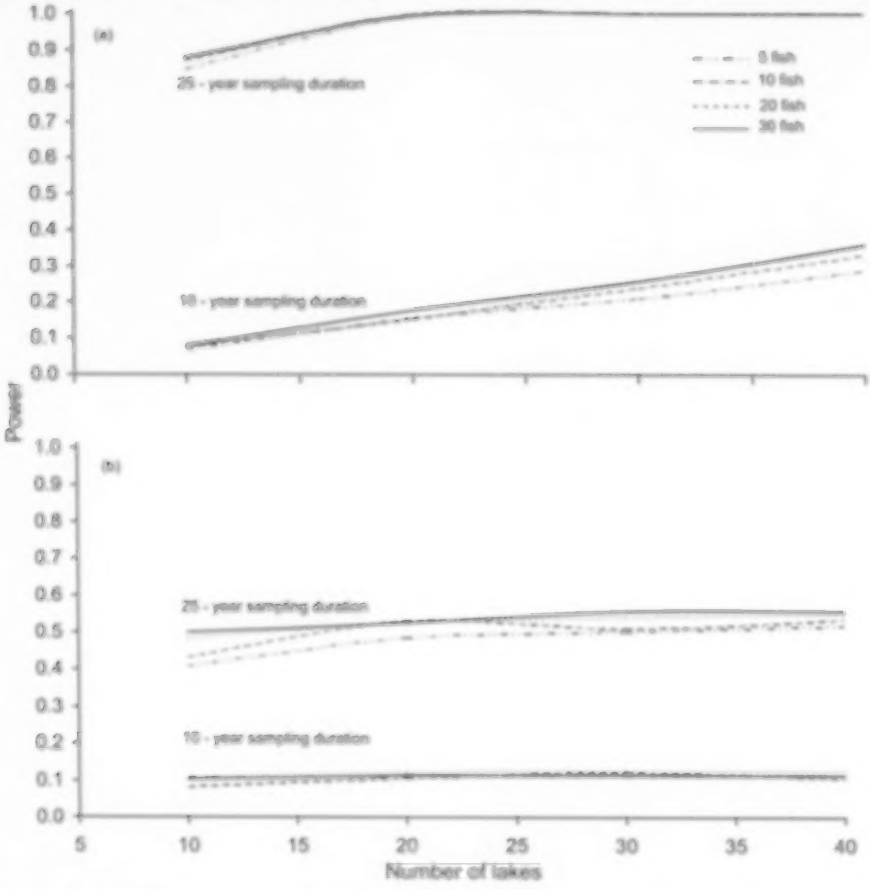
Fig. 3. Power curves for detecting temporal trends in mean length at age for age 4 walleye (*Sander vitreus*) in Michigan (*a*) and Wisconsin (*b*) inland lakes as a function of the number of lakes sampled each year out of a population of 50 lakes and the number of fish sampled from each lake ($\lambda = -1.0$ mm·year^{-1}) for a 10- (bottom set of curves) and 25- (top set of curves) year sampling duration.



ble for the observed trend. Decreases in mean length at age for walleye could be due to effects of anglers or stocking programs. For example, if stocking rates increased over time or if fish numbers increased for some other reason, then increasing competition for resources could lead to reduced growth rates. This mechanism was also proposed by Li et al. (1996) to explain reduced mean weights of walleye in stocked lakes in Minnesota. However, the observed trends could be due to interactions of changing biotic and abiotic conditions over time, which make it difficult to attribute causality to any single source.

Variance components

The proportion of total variance attributed to each component varied considerably among the six data sets we examined. Across all six data sets, residual variation (variation due to sampling error) composed the largest percentage ($\bar{x}$ = 54%) of the total variance, while lake-to-lake and ephemeral temporal averaged 25% and 17% of the total variation, respectively. In contrast, coherent temporal variation and trend variation averaged only 3% and 0.1%, respectively. Furthermore, coherent temporal variation was only significantly different from zero in three out of six analyses, while trend variation was only significant in two analyses (likelihood ratio test, $P < 0.05$). However, our variance estimates are within the percentages reported by Osenberg et al. (1988). Osenberg et al. (1988) partitioned variance in annual increment in length of bluegill and pumpkinseed into four components: residual error, lake, year, and lake × year. On average, residual error variance composed 69% of the total variance, whereas, lake-to-lake variability and lake × year variation composed an average of 20% of the total variance. They found that year effects (coherent variation) did not explain any of the variance. For our analyses, the relatively high residual variation is likely due to measurement error (e.g., errors made during the reading of scales for age determination), variation among individual fish, errors in data processing, crew effects, and collection protocol sampling errors that may have occurred over the time period we examined.

Examining variance structures of monitoring indices has been performed for several lake indicators, primarily using data obtained from the United States Environmental Protection Agency's Environmental Monitoring and Assessment Program (EMAP) in the northeastern USA. The EMAP collected data on a wide range of chemical and biological data,

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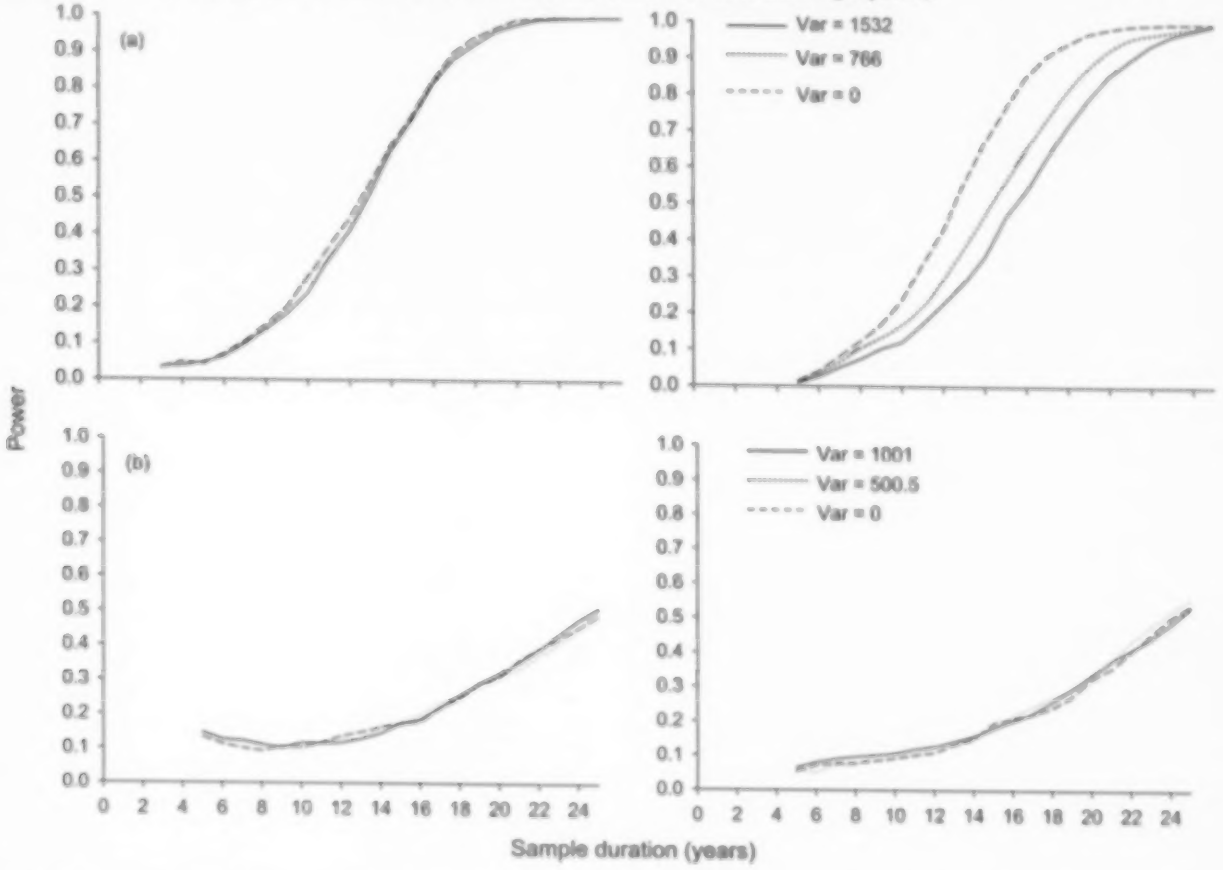
Fig. 4. Power curves for detecting temporal trends in mean length at age for age 4 walleye (*Sander vitreus*) in Michigan (*a*) and Wisconsin (*b*) inland lakes. Lake-to-lake variance is shown at the estimated value from historical data (solid line), decreased by 50% (dotted line), and set to zero (longer dashed line) ($\lambda = -1.0$ mm·year^{-1}, 30 lakes sampled each year, 10 fish sampled per lake). Power curves represent a scenario when 60% of the population of lakes is sampled each year (population of 50 lakes, left panels) or a scenario when 3% of the population of lakes is sampled each year (population of 1000 lakes, right panels).



including water chemistry measures of conservative and nonconservative ions and biological measures such as fish and zooplankton species richness (Stemberger et al. 2001; Kincaid et al. 2004). The variance structures in our analysis of fish mean length at age were within the ranges for zooplankton abundance indicators from the EMAP described by Stemberger et al. (2001), although these authors did not estimate slope variation in their study. For zooplankton abundance indicators, percent lake-to-lake variation ranged from 0% to 69%, coherent temporal variation was "small or negligible", ephemeral temporal variation ranged from 0% to 16%, and residual variation ranged from 14% to 43% (Stemberger et al. 2001).

For some biological indicators, such as fish mean length at age in our study and zooplankton abundances and species richness estimated for the EMAP data, the proportion of residual variance is much higher compared with conservative chemical indicators, such as calcium and magnesium (Kincaid et al. 2004). For conservative chemical indicators, lake-to-lake variation composes a majority of the total variation, and there is relatively low residual variance (Kincaid et al. 2004). The high spatial variation among lakes and low residual variation for conservative ions likely reflects the relative stability of these indicators within lakes over time and space compared with nutrients and biological measurements that are controlled more by within-lake processes and which are more prone to sampling error (e.g., have higher within-lake spatial and temporal variation). These differences between conservative chemical indicators and biological indicators need to be acknowledged and incorporated into the expectations of monitoring programs. For example, detecting a prespecified trend for a biological indicator with a large residual variance component will require a longer sampling period compared with indicators with lower residual variances to detect the same trend, all else being equal. While it might be possible to reduce sampling errors associated with biological indicators, this often may not be the best choice unless little cost is involved (see Power analysis below).

Power analysis

We observed the expected increase in power with increasing trend magnitude and number of years sampled for both the Michigan and Wisconsin analyses. This pattern was also

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Table 4. Mean percent increase in statistical power due to setting the estimated residual and coherent yearly variance to 50% and 25% of estimated values.

	Residual variance		Coherent temporal variance		Coherent temporal and residual variance
	50%	25%	50%	25%	25%
Mean percent increase	3	5	35	95	103

Note: The power estimates correspond to a temporal trend of –1.0 mm·year^{-1} in mean length at age for age 4 walleye (*Sander vitreus*) sampled in Wisconsin inland lakes. The mean percent increase reported is the average percent increase in power over the sampling period (5–25 years) compared with a situation using the estimated variance components from historical data (see Table 3 for variance estimates; population of lakes = 50, 30 lakes sampled each year for 25 years, 10 fish sampled per lake).

demonstrated using the EMAP data (Urquhart et al. 1998). A striking difference between the Michigan and Wisconsin power analyses, however, was the overall low power observed for the Wisconsin data. We expected power to be lower for the Wisconsin analyses because of the higher proportional and absolute value of the estimated coherent temporal and residual variation compared with the Michigan analyses (see below), but we were not certain as to the relative affects of each component (coherent temporal or residual) on power. Furthermore, because Urquhart et al. (1998) demonstrated the importance of coherent temporal variance in reducing trend detection, we wanted to examine its relative effect compared with the much greater proportion of variance attributed to sampling error. To examine this in more detail, we performed a sensitivity analysis using the Wisconsin data. Again, because the Wisconsin variance components that differed most from the Michigan data set were the residual variance (composing 76% of the total variation for Wisconsin ($\hat{\sigma}_r^2 = 4936$) versus 18% for Michigan ($\hat{\sigma}_r^2 = 550$) and coherent temporal variance (composing 4% of the total variation for Wisconsin ($\hat{\sigma}_{ct}^2 = 261$) versus nonsignificant for Michigan), we concentrated our sensitivity analysis on these two components. We set both the residual and coherent temporal variance to 50% and 25% of the estimated values while holding all other variance components at their estimated values. We then reduced them simultaneously while holding all other variances at their estimated values and calculated the mean percent increase in power compared with the baseline situation when only estimated values were used. We report the mean percent power increase representing the average percent increase in power over the sampling period (5–25 years) compared with a situation using the estimated variance components. The mean percent change was calculated as

$$(2)\quad \left\{\sum_{i=5}^{25}\left[(\text{power\_reduced}_i - \text{power\_full}_i)/(\text{power\_full}_i)\times 100\right]\right\}/21$$

Where power_reduced$_i$ is the power to detect a –1.0 mm·year^{-1} trend under the scenario of reduced residual or coherent temporal variation in year i, and power_full$_i$ is the power to detect the same trend under the scenario using the estimated variance components from eq. 1 in year i.

The sensitivity analysis revealed that the coherent temporal variation had a large effect on the power to detect trends (Table 4). Reducing the coherent temporal variation to 50% and 25% of the estimated value led to an average percent increase in power of 35% and 95%, respectively. Conversely, setting the residual variance to 50% and 25% of estimated values led to only 3% and 5% increases in power, respectively. Thus, even though coherent temporal variation composed only 4% of the total variation for Wisconsin and residual variation composed 75% of Wisconsin's total variation, coherent temporal variation had a disproportionately large influence on the power to detect trends. However, once the coherent temporal variance was set to 25% of the estimated value, setting the residual variance to 25% of the estimated value did lead to a slightly larger increase in power, a further 8% increase over the baseline estimates when compared with just setting coherent temporal variance to 25% of estimated value. Although it is unknown why coherent temporal variance was large for the Wisconsin analysis, possible sources of this coherent variation include factors that impact fish populations at a regional scale, such as annual differences in temperature.

We further investigated the relatively large coherent temporal variation for the Wisconsin data by examining the magnitude of best linear unbiased predictors for year effects. Our examination showed that the relatively high variance for the Wisconsin data set was not due to one or a few years, but rather a generally broader distribution of year effects. We examined data for years in the Wisconsin data set that had large effects (i.e., those years with greater than 1 standard deviation from the mean) to see if they differed from other years in the number of lakes sampled. Years that had large effects were often years when very few lakes were sampled or for years where a number of the sampled lakes were not sampled in any other year (i.e., few revisited sites). However, it is difficult to generalize as to why some years showed a large effect while others did not, because there were also years with small effects that were characterized by these same sample characteristics, including some years in the Michigan data set, where coherent variation was much less.

The strong effect of temporal coherent variation to reduce trend detection capabilities was also demonstrated by Urquhart et al. (1998). Because this source of temporal variation cannot be reduced by changing the design of a monitoring program, only an increased sampling duration will lead to an increase in statistical power (Urquhart et al. 1998; Kincaid et al. 2004). This example illustrates the importance

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of examining variance components of potential monitoring indices, because even a small (as estimated as percentage of the total variation) coherent temporal variation component can reduce trend detection capabilities over the short term.

Although coherent temporal variation can greatly reduce power, the power to detect trends can also be affected by the allocation of resources to either sample more lakes per year or sample more fish per lake. The effect of increasing the number of lakes sampled each year versus increasing the number of fish sampled from each lake on the power to detect trends is important from a management perspective because this issue represents a resource allocation trade-off. Our analysis suggested that very modest samples within lakes will often be adequate and that often the focus should be placed on sampling more lakes rather than more or better at each lake. Others have previously argued that sampling more locations rather than more sampling at a location would often be a better approach for improving power (e.g., Larsen et al. 2004).

High lake-to-lake (spatial) variance has been shown to reduce the power to detect trends (e.g., Urquhart et al. 1998). In our analysis, the relative importance of lake-to-lake variance was dependent on the proportion of lakes sampled from the population of lakes each year. For example, in our power analysis based on the age 4 walleye Michigan data, we were able to obtain a better estimate of lake-to-lake variance when we sampled 60% of the lakes each year compared with sampling 3% of the lakes each year. Consequently a reduction in lake-to-lake variance did not have an appreciable effect on power under the 60% sampling scenario. However, when sampling only 3% of the population of lakes each year, lake-to-lake variation became more important, and reductions in this source of variation led to an increase in power. Thus, in situations with a large lake-to-lake variance component, it is advisable to consider designs that incorporate planned repeated sampling at some lakes so as to factor out some of the lake-to-lake variance and increase power, without having to sample a majority of the lakes in the region (see references for detailed discussion of sampling designs for trend detection and this issue). Furthermore, if repeated visits are not built into the design, sampling from a large population of lakes may limit what variance components are even estimable, as we saw for both actual and simulated data sets. Although it was not within the scope of this paper to explore the many alternative sampling designs, the type of sampling design employed, such as the use of fixed sites in combination with a random selection of lakes each year, can affect power to detect trends (Urquhart et al. 1998). With information on the components of variance for desired monitoring indices, management agencies can explore alternate designs in an effort to maximize power.

The use of historical data from state and federal agencies provides one source of data that can be used to investigate the presence of trends in fisheries data for multiple populations (e.g., this study; Reckahn 1986; Beard and Kampa 1999). Much of the historical data, however, were not collected following probability sampling methods, in which every sampling unit has a known probability of being sampled (Olsen et al. 1999). Rather, water bodies were often sampled based on expert choice (i.e., judgment sampling; Olsen et al. 1999), selected by convenience, or in response to local or regional political concerns (e.g., convenience sampling; Olsen et al. 1999). The nonprobability-based sampling associated with the historical data weakens the strength of the statistical inferences to the population of lakes or streams as a whole. Nevertheless, these data provide a unique opportunity to examine regional trends. Furthermore, because the implementation of probabilistic sampling designs is only now becoming more prevalent, historical data often represent the only source of information that can be used for the development of monitoring programs designed to describe the status of systems and to detect trends of aquatic indices.

Although the statistical power to detect trends is important to consider when developing a monitoring program, there are other components of a monitoring program that should also be considered. For example, the costs and benefits of implementing a monitoring design should be considered along with the uncertainties associated with alternative designs (MacGregor et al. 2002). Thus, power analysis represents one source of information to be used in the processes of designing an ecological monitoring program. Examining variance components of desired indices, power analysis, and other quantitative analyses that take into account uncertainties and expected benefits of monitoring programs represents powerful tools that will help fisheries management agencies develop effective monitoring programs.

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References

Antonopoulos, V.Z., Papamichail, D.M., and Mitsiou, K.A. 2001. Statistical and trend analysis of water quality and quantity data for the Strymon River in Greece. Hydrol. Earth Syst. Sci. **5**: 679–691.

Beard, D.T., and Kampa, J.M. 1999. Changes in bluegill, black crappie, and yellow perch populations in Wisconsin during 1967–1991. N. Am. J. Fish. Manag. **19**: 1037–1043.

Claramunt, R.M., and Wahl, D.H. 2000. The effects of abiotic and biotic factors in determining larval fish growth rates: a comparison across species and reservoirs. Trans. Am. Fish. Soc. **129**: 835–851.

Fairweather, P.G. 1991. Statistical power and design requirements for environmental monitoring. Aust. J. Mar. Freshw. Res. **42**: 555–567.

Grant, G.C., Schwartz, Y., Weisberg, S., and Schupp, D.H. 2004. Trends in abundance and mean size of fish captured in gill nets from Minnesota lakes, 1983–1997. N. Am. J. Fish. Manag. **24**: 417–428.

Hatch, S.A. 2003. Statistical power for detecting trends with applications to seabird monitoring. Biol. Conserv. **111**: 317–329.

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Hayes, D., Baker, E., Bednarz, R., Borgeson, D., Jr., Braunscheidel, J., Breck, J., Bremigan, M., Harrington, A., Hay, R., Lockwood, R., Nuhfer, A., Schneider, J., Seelbach, P., Waybrant, J., and Zorn, T. 2003. Developing a standardized sampling program: the Michigan experience. Fisheries, **28**: 18–25.

He, J.X., and Bence, J.R. 2007. A comparison among methods for modeling annual growth variations based on the von Bertalanffy growth function, with applications to lake trout in southern Lake Huron. Trans. Am. Fish. Soc. **136**: 318–330.

Jassby, A.D., Goldman, C.R., Reuter, J.E., and Richards, R.C. 1999. Origins and scale dependence of temporal variability in transparency of Lake Tahoe, California–Nevada. Limnol. Oceanogr. **44**: 282–294.

Kincaid, T.M., Larsen, D.P., and Urquhart, N.S. 2004. The structure of variation and its influence on the estimation of status: indicators of condition of lakes in the northeast, U.S.A. Environ. Monit. Assess. **98**: 1–21.

Larsen, D.P., Urquhart, N.S., and Kugler, D.L. 1995. Regional scale trend monitoring of indicators of trophic condition of lakes. Water Resour. Bull. **31**: 117–140.

Larsen, D.P., Kincaid, T.M., Jacobs, S.E., and Urquhart, N.S. 2001. Designs for evaluating local and regional scale trends. Bioscience, **51**: 1069–1078.

Larsen, D.P., Kaufmann, P.K., Kincaid, T.M., and Urquhart, N.S. 2004. Detecting persistent change in the habitat of salmon-bearing streams in the Pacific Northwest. Can. J. Fish. Aquat. Sci. **61**: 283–291.

Li, J., Cohen, Y., Schupp, D.H., and Adelman, I.R. 1996. Effects of walleye stocking on population abundance and fish size. N. Am. J. Fish. Manag. **16**: 830–839.

Littell, R.C., Milliken, G.A., Stroup, W.W., and Wolfinger, R.S. 1996. SAS system for mixed models. SAS Institute Inc., Cary, N.C.

MacGregor, B.W., Peterman, R.M., Pyper, B.J., and Bradford, M.J. 2002. A decision analysis framework for comparing experimental designs of projects to enhance pacific salmon. N. Am. J. Fish. Manag. **22**: 509–527.

McDonough, T.A., and Buchanan, J.P. 1991. Factors affecting abundance of white crappies in Chickamauga Reservoir, Tenessee, 1970–1989. N. Am. J. Fish. Manag. **11**: 513–524.

Olsen, A.R., Sedransk, J., Edwards, D., Gotway, C.A., Liggett, W., Rathbun, S., Reckow, K.H., and Young, L.J. 1999. Statistical issues for monitoring ecological and natural resources in the United States. Environ. Monit. Assess. **54**: 1–45.

Osenberg, C.W., Werner, E.E., Mittelbach, G.G., and Hall, D.J. 1988. Growth patterns in bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) sunfish: environmental variation and the importance of ontogenetic niche shifts. Can. J. Fish. Aquat. Sci. **45**: 17–26.

Peterman, R.M. 1990. Statistical power analysis can improve fisheries research and management. Can. J. Fish. Aquat. Sci. **47**: 2–15.

Piepho, H.-P., and Ogutu, J.O. 2002. A simple mixed model for trend analysis in wildlife populations. J. Agric. Biol. Environ. Stat. **7**: 350–360.

Quist, M.C., Guy, C.S., Schultz, R.D., and Stephen, J.L. 2003. Latitudinal comparisons of walleye growth in North American and factors influencing growth of walleyes in Kansas reservoirs. N. Am. J. Fish. Manag. **23**: 677–692.

Reckahn, J.A. 1986. Long-term cyclical trends in growth of lake whitefish in South Bay, Lake Huron. Trans. Am. Fish. Soc. **115**: 787–803.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. Bull. 191.

Sandén, P., and Håkansson, B. 1996. Long-term trends in Secchi depth in the Baltic Sea. Limnol. Oceanogr. **41**: 346–351.

Sass, G.G., Hewett, S.W., Beard, T.D., Jr., Fayram, A.H., and Kitchell, J.F. 2004. The role of density dependence in growth patterns of ceded territory walleye populations of northern Wisconsin: effects of changing management regimes. N. Am. J. Fish. Manag. **24**: 1262–1278.

Self, S., and Liang, K.-Y. 1987. Asymptotic properties of maximum likelihood estimators and likelihood ratio tests under nonstandard conditions. J. Am. Stat. Assoc. **82**: 605–610.

Stemberger, R.S., Larsen, D.P., and Kincaid, T.M. 2001. Sensitivity of zooplankton for regional lake monitoring. Can. J. Fish. Aquat. Sci. **58**: 2222–2232.

Stow, C.A., Carpenter, S.R., Webster, K.E., and Frost, T.M. 1998. Long-term environmental monitoring: some perspectives from lakes. Ecol. Appl. **8**: 269–276.

Szalai, E.B., Fleischer, G.W., and Bence, J.R. 2003. Modeling time-varying growth using a generalized von Bertalanffy model with application to bloater (*Coregonus hoyi*) growth dynamics in Lake Michigan. Can. J. Fish. Aquat. Sci. **60**: 55–66.

Trippel, E.A. 1993. Relations of fecundity, maturation, and body size of lake trout, and implications for management in northwest Ontario lakes. N. Am. J. Fish. Manag. **13**: 64–72.

Urquhart, N.S., and Kincaid, T.M. 1999. Designs for detecting trend from repeated surveys of ecological resources. J. Agric. Biol. Environ. Stat. **4**: 404–414.

Urquhart, N.S., Paulsen, S.G., and Larsen, D.P. 1998. Monitoring for policy-relevant regional trends over time. Ecol. Appl. **8**: 246–257.

VanLeeuwen, D.M., Murray, L.W., and Urquhart, N.S. 1996. A mixed model with both fixed and random trend components across time. J. Agricult. Biol. Environ. Stat. **4**: 435–453.

Vaughan, H., Brydges, T., Fenech, A., and Lumb, A. 2001. Monitoring long-term ecological changes through the ecological monitoring and assessment network: science-based and policy relevant. Environ. Monit. Assess. **67**: 3–28.

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Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality?

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Abstract: The relationships among behavior, environment, and migration success in anadromous fishes are poorly understood. We monitored migration behavior at eight Columbia and Snake river dams for 18 286 adult Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (sea-run *Oncorhynchus mykiss*) over 7 years using radiotelemetry. When statistically controlling for variation in flow, temperature, fisheries take, and other environmental variables, we observed that unsuccessful individuals — those not observed to reach spawning areas — had longer passage times at nearly all dams than fish that eventually reached tributaries. In many cases, times were also longer for unsuccessful adults passing through a multiple-dam reach. Four ecological mechanisms may have contributed to these patterns: (*i*) environmental factors not accounted for in the analyses; (*ii*) inefficient responses by some fish to passage conditions at dams that resulted in slowed passage, energetic depletion, and unsuccessful migration; (*iii*) ongoing selection for traits needed to pass obstructions; and (or) (*iv*) passage rate was not directly linked to migration success, but rather, both resulted from relatively poor phenotypic condition upon river entry in unsuccessful migrants. Overall, these results illustrate the need for a mechanistic understanding of the factors that influence migration success and the need for fitness-based criteria to assess the effects of dams on anadromous fishes.

Résumé : On connaît mal les relations entre le comportement, l'environnement et le succès de la migration chez les poissons anadromes. Nous avons suivi par télémétrie le comportement migrateur de 18 286 saumons chinook (*Oncorhynchus tshawytscha*) et truites arc-en-ciel anadromes (*Oncorhynchus mykiss*) adultes à huit barrages sur le fleuve Columbia et la rivière Snake sur une période de 7 ans. Une fois que nous avons tenu compte statistiquement des variations de débit, de température, de retraits dus à la pêche et des autres variables du milieu, nous observons que les individus qui échouent leur migration — qui n'ont pas été observés sur les sites de fraye — prennent plus de temps pour traverser presque tous les barrages que les poissons qui éventuellement atteignent les tributaires. Dans plusieurs cas, le temps de passage dans les sections avec plusieurs barrages est aussi plus long pour les adultes qui échouent leur migration. Quatre mécanismes écologiques peuvent contribuer à ces patrons: (*i*) des facteurs écologiques non considérés dans les analyses, (*ii*) des réactions inefficaces de certains poissons aux conditions de traversée des barrages qui ont pour résultat de ralentir la traversée, d'épuiser les réserves énergétiques et de faire échouer la migration, (*iii*) une sélection actuelle des caractéristiques nécessaires pour surmonter les obstacles et (ou) (*iv*) des taux de passage qui ne sont pas reliés directement au succès de la migration, les deux variables s'expliquant plutôt par une mauvaise condition phénotypique lors de l'entrée dans la rivière chez les poissons qui échouent leur migration. Dans leur ensemble, nos résultats indiquent qu'il est nécessaire d'obtenir une compréhension mécaniste des facteurs qui influencent le succès de la migration, ainsi que des critères basées sur la fitness pour évaluer les effets des barrages sur les poissons anadromes.

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Introduction

The single greatest change to rivers worldwide since the industrial revolution has been the construction of nearly 50 000 dams higher than 15 m (Hart and Poff 2002; Poff and Hart 2002; Postel and Richter 2003). Dams have long been recognized as obstacles to fish migration, and slowed migration or "delay" at dams has been observed in many fish species, including Atlantic salmon (*Salmo salar*) (Karppinen et al. 2002), barbel (*Barbus barbus*) (Lucas and Frear 1997), American shad (*Alosa sapidissima*) (Moser et al. 2000), sea lamprey (*Petromyzon marinus*) (Haro and Kynard 1997), paddlefish (*Polyodon spathula*) (Zigler et al. 2004), and salmonids (*Oncorhyncus* spp.) of the Columbia River Basin (Williams 1998; Keefer et al. 2004*a*). Dams have frequently been implicated in the decline of resident and anadromous fish populations, in part because of their effects on adult migration (e.g., NRC 1996; Northcote 1998; Dudgeon 2003). Unfortunately, primarily because of logistical constraints, the large body of literature on adult fish passage behavior and performance has been conducted primarily at small scales or at single dams (e.g., Clay 1995; Hinch and Bratty 2000; Bunt et al. 2001), and few studies have examined the relationship between slowed migration and eventual migration success upstream (Naughton et al. 2005).

Similar to many anadromous fishes in regulated rivers, adult Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (sea-run *Oncorhynchus mykiss*) returning to spawning tributaries of the Columbia and Snake rivers must ascend multiple dams (up to nine; Fig. 1). Construction of the Columbia–Snake hydrosystem has been identified as one of several factors causing the decline and listing of more than a dozen salmon and steelhead evolutionary significant units (species, subspecies, geographic races, or populations considered as separate entities for conservation) under the US Endangered Species Act (NRC 1996; Ruckelshaus et al. 2002). Adult fish passage facilities at Columbia and Snake river dams were explicitly designed for the passage of salmonids, and their basic design has been continually refined to enhance their ability to attract and pass both salmonids and nonsalmonid fishes (Monk et al. 1989; Bell 1991; Moser et al. 2002*a*).

Despite the presence of fish passage facilities and efforts to improve migration conditions at dams, concern remains that slowed migration may have direct or indirect negative effects on adult salmon migration and reproductive success. In the Columbia–Snake system, most adult salmonids pass each dam within 2 days of entering the tailrace and eventually reach spawning tributaries (Keefer et al. 2004*a*, 2005). However, 1.4%–13.7% of individuals in each run have taken more than 5 days to pass single dams, and some fish take several weeks to pass (Keefer et al. 2004*a*). Adult salmonids rely on energy reserves gained in the marine environment for migration, suggesting the potential for relatively slow passage to incur a fitness cost. For instance, Geist et al. (2000) estimated that migrating fall Chinook salmon in the Columbia River requiring more than 5 days to pass each dam may have insufficient energy reserves to complete spawning. Whether migratory delay at dams contributes to reduced fitness in anadromous fishes in general or hinders the recovery of Columbia Basin salmonids in particular has been a lingering question since the construction of dams with fishways. Determining how migration behavior at dams (as measured by passage time) relates to upstream fate is important to understanding how widespread delayed or carry-over effects may be in the ecology of adult anadromous fishes.

Fig. 1. Map of the study region, including location of dams. Fish were collected and tagged at Bonneville Dam. Upstream migration to spawning sites was monitored as far upstream as river kilometre (rkm) 1300 in the Snake River basin or Wells Dam on the Columbia River using 150–170 fixed site antennas and mobile tracking in boats and trucks. Distances from the Columbia River mouth are given parenthetically as rkm. Abbreviations for Lower Columbia River dams: BO, Bonneville; JD, John Day; TD, The Dalles; MN, McNary. Abbreviations for Snake River dams: IH, Ice Harbor; LM, Lower Monumental; GO, Little Goose; GR, Lower Granite; HC, Hells Canyon (impassible); DW, Dworkshak Dam (Clearwater River).

During seven migration seasons from 1996 to 2003, we radio-tagged 18 286 returning adult salmonids in four runs (defined by adult return date as spring, summer, and fall Chinook salmon, and summer steelhead). Each run was composed of one or more evolutionary significant units. The general aim of the research has been to identify passage problems and potential solutions. Previously, we have presented general patterns of survival and migration through the hydrosystem (Keefer et al. 2005; Goniea et al. 2006; High et al. 2006) and migration behavior at individual dams and hydrosystem segments (Keefer et al. 2004*a*, 2004*b*; Naughton et al. 2005), in tributaries (Keefer et al. 2004*c*), and in relation to specific passage issues (e.g., Reischel and Bjornn 2003; Boggs et al. 2004; Johnson et al. 2005).

In this study, we tested for an association between fish passage time and eventual fate at two scales: passage at individual dams in the lower Columbia and Snake rivers and total passage time past four dams and through three reservoirs in the lower Columbia hydrosystem. At the first scale, we used Cox proportional hazards regression (PHReg; Allison 1995; Hosmer and Lemeshow 1999) to analyze passage time at each dam in relation to eventual fate while statistically accounting for variation in river environment and fish traits insomuch as possible. PHReg is particularly well suited to the analysis of passage time data (Castro-Santos and Haro

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2003), because the method readily handles cases with incomplete records by censoring and incorporates time-varying covariates — predictor variables whose values are allowed to vary during individual passage events (i.e., river discharge or light level). At the second scale, we used linear models to test whether mean passage times differed between successful and unsuccessful migrants ascending a reach of the lower Columbia River hydrosystem that included four dams and three reservoirs. Overall, the analyses revealed consistent associations between relatively long passage times and eventually unsuccessful migration at both scales. We used results from these two analyses to identify potential underlying mechanisms affecting migration success in anadromous fishes.

Materials and methods

Study system

The Columbia River is the third-largest river system in North America, draining an area of 671 000 km^2, including nearly all of Idaho and large areas of Oregon, Washington, Montana, and British Columbia (Fig. 1). Mean annual discharge at the river's mouth is approximately 6650 m^3·s^{-1}. Fish returning to Snake River drainages must pass the four lower Columbia River dams and most also pass the four lower Snake River dams (Fig. 1). Those returning to Columbia River sites upstream from the Snake River confluence pass a total of four to nine dams. As fish migrate upstream, they encounter 1–2 km long tailraces below dams with turbulent flow caused by discharge from dam turbines and spillways. Fish must distinguish relatively low volume attraction flows leading to fishway entrances at dam faces from the large discharge of turbines and spillways. Once in collection channels, fish pass through transition pools and into ladders, which may be up to 1300 m long, gain 35 m in elevation, and contain 75 or more weirs and pools (Williams 1998).

Most spring and summer Chinook salmon returning to the Snake River basin and lower Columbia River tributaries are stream type Chinook, spending their first year rearing in freshwater before migrating seaward in the spring and summer of their second year. Most adults return after three winters at sea, with some returning after two and four winters (jacks, or precocious males returning after one winter, were not included in this study). Adult fall Chinook salmon return in late summer and early fall, and most spawn in the mainstem Columbia and Snake rivers, especially the 70 km Hanford Reach below Priest Rapids Dam, the only remaining free-flowing stretch of the Columbia River accessible to anadromous fishes upstream from Bonneville Dam. Fall Chinook are ocean type Chinook salmon, as are some summer-run Chinook salmon, migrating to sea in their first year (age 0), returning after two to five winters at sea at age three to six. Steelhead adults may return in any month, though the majority of interior Columbia Basin steelhead enter fresh water in summer and fall and spawn the following spring. Juvenile steelhead reside in fresh water for at least 2 years before outmigrating in spring. Adult steelhead typically return to spawn after one to two winters at sea, and a small proportion (<10%) are iteroparous.

Radio-tagging, telemetry monitoring, and fate assignment

The methods used to radio-tag and monitor salmonid migration and assign fates to individual fish in the Columbia and Snake river basins have been described in detail in Keefer et al. (2004*a*, 2005). Briefly, fish were diverted from the Washington Shore fish ladder at Bonneville Dam (river kilometre (rkm) 235) into a facility where they could be selected by species. During fall, we targeted "upriver bright" Chinook salmon, a group generally defined as originating east of the Cascade Range; however, run assignment based on timing may have resulted in the inclusion of some ocean-type summer Chinook salmon and tule fall Chinook salmon returning to lower Columbia River tributaries and hatcheries. Diverted fish were anesthetized, sexed, measured for fork length, and inspected for the presence of fin clips indicating known hatchery origin. All fish were tagged with a gastrically implanted radiotransmitter (Lotek Wireless, Inc., Newmarket, Ontario). Prior to 2000, all fish were released about 9.5 km downstream of Bonneville Dam near Dodson, Oregon, or Skamania, Washington. During 2000–2002, 23.2% of spring Chinook salmon, 23.9% of summer Chinook salmon, 35.1% of fall Chinook salmon, and 27.9% of steelhead were released in the Bonneville forebay to meet other study objectives; the remainder were released at the downstream sites. In all years, secondary tags, including passive integrated transponder tags (PIT tags), were used to estimate rates of transmitter loss, which averaged 2.2%–4.0%, depending on species (Keefer et al. 2004*d*). Individuals with records indicating lost tags were excluded from all analyses.

Adult migration behavior in the Columbia Basin was monitored using an extensive array of approximately 160 radio receiver sites at dams and in tributaries (detailed in Moser et al. 2002*b*; Reischel and Bjornn 2003; Naughton et al. 2005). Behavior at dams was monitored using fixed aerial and underwater antennas in tailraces and fishways. Major tributaries were monitored with fixed aerial antennas near tributary mouths and with mobile tracking units attached to trucks and boats. Additional data were collected from voluntary returns of transmitters from fisheries (US$25–$100 rewards) and from cooperative returns from hatcheries, weirs, and spawning ground surveys operated by federal, state, and tribal agencies.

We used these data to classify individual fish as having reached potential spawning sites (successful migrants), having unknown fates (unsuccessful migrants) as in Naughton et al. (2005), or as fisheries take in the main stem Columbia or Snake rivers. Successful migrants included salmon with telemetry records in known spawning tributaries, those found as carcasses in spawning ground surveys, or those that returned to their hatchery of origin. Beginning in 2000, we were able to identify straying in a subset of radio-tagged adults that had been PIT-tagged during the juvenile stage (i.e., fish of known origin). Strays were identified as known-origin adults having final records in non-natal spawning tributaries. Straying rates were generally low during 2000–2003 (2.2% spring–summer Chinook salmon, n = 1588; 4.2% fall Chinook salmon, n = 166; 6.8% steelhead, n = 1414; M.L. Keefer, C.A. Peery, J. Firehammer, and M.L. Moser, unpublished data), and in the context of this study, we conserva-

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tively considered strays to be successful migrants by presuming these individuals had reached potential spawning tributaries. Unsuccessful migrants were salmon with unknown fates whose final telemetry records were outside spawning sites, usually at or between dams, and presumably represent prespawn mortalities, though this group may have included unreported harvest or fish that went undetected in monitored tributaries. Whether fish captured in fisheries would have successfully migrated remains unknown, and hence these fish were excluded from all analyses. We felt these operational definitions accurately represented the fates of the vast majority of fish for several reasons. The rate of transmitter loss through regurgitation was low (Keefer et al. 2004*d*). The linear nature of the study system, the large number of antenna sites used, and large mobile tracking efforts provided a high probability of detection, particularly at dams. For instance, Naughton et al. (2005) estimated the probability of an individual passing two dams in the mid-Columbia River undetected at $<1.0 \times 10^{-7}$ based on the minimum number of fixed-site receivers salmon passed at these dams and frequencies of receiver outages. While many fish went undetected at individual antennas, it was improbable that misclassification of fates seriously biased our results overall, because any misclassification should act to minimize observed differences in passage behavior between fate groups, rather than create false differences.

Data analysis

For all analyses, we defined passage time as the time elapsed from the first detection at a tailrace antenna 0.5–2 km downstream from the face of a dam to the last record at a fish ladder exit antenna. We conservatively used times for first ascents only at each dam for those fish that fell back downstream (Boggs et al. 2004) and reascended because of the potential for learning or injury to affect subsequent passage times. Other measures of passage time, such as first approach or first entrance to ladder exit, provided qualitatively similar results (C.C. Caudill, unpublished data).

Passage time at individual dams

We used PHReg (Allison 1995; Hosmer and Lemeshow 1999; Castro-Santos and Haro 2003) to model the relationships among observed passage times at individual dams, fate, and other predictor variables using widely available software (PROC PHREG in SAS v.9, SAS Institute Inc., Cary, North Carolina). PHReg models the probability of an event occurring (dam passage) for an individual within a very small time interval as a passage hazard given (*i*) that the event had not occurred prior to the beginning of the time interval and (*ii*) a set of predictor variables such as river discharge level and temperature at the beginning of the time interval. Increasing passage hazard corresponds to more rapid passage and shorter passage times. Passage hazards for different groups are expressed as odds ratios; an odds ratio of 2.0 for successful vs. unsuccessful adults indicates successful adults were twice as likely to pass during a time interval as unsuccessful adults. An odds ratio of 1.0 indicates no difference in probability. We modeled passage hazard in relation to fish fate and environmental factors (flow, temperature, etc.) and fish traits (length, sex, etc.) known to affect migration behavior. The primary advantages of the PHReg method are that it allows predictor variables to vary through time, the censoring of individuals, and the software is widely available. The inability to estimate mean differences in passage time represents the primary disadvantage of the PHReg approach. Other parametric approaches to the analysis of time-event data are available, but do not allow time-varying covariates, require assumptions about the form of the survival function (Allison 1995; Castro-Santos and Haro 2003), or allow time-varying covariates, but currently do not incorporate tests among groups (Moser et al. 2005).

Prior to analysis, we identified a set of 15 candidate models, each consisting of 2–14 predictor variables describing variation in passage environment, fish traits, and individual fate (Table 1; Supplemental Appendix S1[1]). River environment was described by daily mean values of total discharge (flow), spill (the amount of water passing over the spillway of dams rather than passing through turbines), and temperature because of the potential effect of these factors on salmon behavior and physiology. River environmental data were obtained from Columbia River DART (2005). Few salmon pass ladders at night (e.g., Naughton et al. 2005), and we included a variable coding day vs. night, adjusted for seasonal changes in day length, to account for diel changes in passage behavior. During some periods with low fish passage density (early spring, late fall, and winter), data from Bonneville and McNary dams and Ice Harbor and Lower Granite dams were used to estimate river values at other Columbia and Snake river dams, respectively, because values among dams were highly correlated (e.g., temperature at Bonneville and McNary dams, 1996–2003: $R^2 = 0.98$). We tested for the potential of high fish densities in ladders to slow passage by including the daily dam count of all salmonids and American shad for each dam as separate variables (DART 2005). The above model covariates were time-varying for each fish; those described below were fixed.

The final fate of the fish was the primary predictor of interest. The Cox proportional hazards model assumes the odds ratio between groups remains constant through time. The inclusion of a fate × passage time interaction both tested for and statistically controlled for deviation from this model assumption (Allison 1995, p. 155). Five additional covariates estimated fish traits: sex, fork length, origin (hatchery or wild), date of tagging as an index of seasonal differences among fish entering the river relatively early or late within each run and (or) unmeasured seasonal trends in environmental variation, and release location (downstream of Bonneville Dam or released to the Bonneville Dam forebay). Interannual differences in river condition have a strong effect on migration behavior (Boggs et al. 2004; Keefer et al. 2004*a*, 2004*b*), and consequently, the analyses were stratified by year. The overall effect of year was tested by comparing models with and without year effects, but unfortunately the quantitative differences among years can

[1] Supplementary data for this article are available on the journal Web site (cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5182. For more information on obtaining material refer to cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

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Table 1. Model-averaged odds ratios and unconditional 95% confidence intervals (CI) from PHReg analyses of passage time at lower Columbia River and Snake River dams.

	Dam							
	Bonneville	The Dalles	John Day	McNary	Ice Harbor	Lower Monumental	Little Goose	Lower Granite
Spring Chinook salmon (*Oncorhynchus tshawytscha*)								
N	3878	2865	2622	2287	1680	1562	1336	1415
Censored	145	228	153	217	110	143	23	46
% Censored	3.7	8.0	5.8	9.5	6.5	9.2	1.7	3.3
Unsuccessful	644	368	276	151	87	53	30	33
% Unsuccessful	16.6	12.8	10.5	6.6	5.2	3.4	2.2	2.3
Estimate								
TOD								
Odds ratio	**0.103**	**0.106**	**0.066**	**0.061**	**0.048**	**0.066**	**0.092**	**0.050**
95% CI	**0.089, 0.120**	**0.089, 0.127**	**0.052, 0.083**	**0.047, 0.080**	**0.034, 0.067**	**0.048, 0.091**	**0.068, 0.124**	**0.035, 0.072**
Flow								
Odds ratio	0.999	0.999	**0.998**	**0.996**	**0.993**	0.997	0.997	1.002
95% CI	0.996, 1.002	0.997, 1.001	**0.996, 1.000**	**0.993, 0.999**	**0.989, 0.998**	0.993, 1.002	0.993, 1.001	0.994, 1.011
Temperature								
Odds ratio	1.042	**1.135**	**1.085**	**1.130**	0.989	1.042	1.025	0.942
95% CI	0.860, 1.262	**1.040, 1.238**	**1.005, 1.170**	**1.025, 1.245**	0.913, 1.070	0.968, 1.123	0.941, 1.117	0.863, 1.029
Spill								
Odds ratio	0.985	0.983	0.984	0.998	0.968	**0.877**	**0.887**	**0.847**
95% CI	0.968, 1.003	0.958, 1.008	0.948, 1.022	0.951, 1.047	0.909, 1.030	**0.818, 0.941**	**0.824, 0.955**	**0.779, 0.920**
Salmon								
Odds ratio	0.968	**1.052**	**1.062**	**1.048**	**1.107**	**1.058**	**1.000**	**1.065**
95% CI	0.931, 1.006	**1.003, 1.104**	**1.016, 1.110**	**1.013, 1.085**	**1.052, 1.164**	**1.012, 1.105**	**1.000, 1.000**	**1.015, 1.116**
Shad								
Odds ratio	0.178	**0.992**	**0.988**	**0.974**	**1.123**	1.096	0.999	0.070
95% CI	0.001, 57.994	**0.984, 0.999**	**0.979, 0.996**	**0.950, 1.000**	**1.005, 1.254**	0.960, 1.251	0.998, 1.000	0.000, 80.522
Release site								
Odds ratio	NA	**1.436**	**1.321**	1.098	1.068	0.970	1.171	**1.236**
95% CI	—	**1.233, 1.672**	**1.127, 1.548**	0.926, 1.302	0.892, 1.279	0.798, 1.178	0.962, 1.425	**1.008, 1.514**
Fate								
Odds ratio	1.096	1.199	**1.292**	**1.494**	**1.566**	1.461	1.112	**2.228**
95% CI	0.953, 1.259	0.993, 1.447	**1.048, 1.593**	**1.154, 1.934**	**1.107, 2.215**	0.911, 2.345	0.538, 2.298	**1.053, 4.715**
Fate × Time								
Odds ratio	**1.079**	**1.136**	**1.089**	1.011	1.040	**1.294**	1.449	1.208
95% CI	**1.044, 1.116**	**1.070, 1.207**	**1.040, 1.140**	0.951, 1.074	0.961, 1.125	**1.012, 1.653**	0.873, 2.405	0.902, 1.618
Sex								
Odds ratio	0.958	**0.908**	0.980	0.989	1.001	1.026	1.088	0.934
95% CI	0.889, 1.032	**0.828, 0.995**	0.894, 1.074	0.893, 1.095	0.891, 1.125	0.903, 1.165	0.957, 1.236	0.825, 1.058
Tag day								
Odds ratio	**1.022**	1.012	1.007	1.004	0.998	0.997	1.007	1.007
95% CI	**1.015, 1.029**	1.000, 1.024	0.998, 1.016	0.995, 1.013	0.990, 1.006	0.988, 1.007	0.997, 1.017	0.994, 1.020

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Table 1 (*continued*).

	Dam							
	Bonneville	The Dalles	John Day	McNary	Ice Harbor	Lower Monumental	Little Goose	Lower Granite
Clipped								
Odds ratio	1.004	1.003	0.936	1.055	0.930	1.096	1.063	0.938
95% CI	0.928, 1.087	0.913, 1.102	0.848, 1.033	0.952, 1.169	0.822, 1.053	0.960, 1.251	0.922, 1.225	0.818, 1.076
Length								
Odds ratio	0.998	**0.991**	**0.989**	**0.987**	1.000	**0.989**	0.992	0.993
95% CI	0.993, 1.003	**0.985, 0.998**	**0.982, 0.996**	**0.980, 0.994**	0.992, 1.009	**0.980, 0.999**	0.982, 1.002	0.983, 1.003
Summer Chinook salmon								
N	1615	1362	1390	1075	299	283	236	244
Censored	40	49	99	169	8	5	3	5
% Censored	2.5	3.6	7.1	15.7	2.7	1.8	1.3	2.0
Unsuccessful	198	150	121	65	8	5	3	3
% Unsuccessful	12.3	11.0	8.7	6.0	2.7	1.8	1.3	1.2
Estimate								
TOD								
Odds ratio	**0.116**	**0.100**	**0.162**	**0.107**	**0.057**	**0.008**	**0.166**	**0.054**
95% CI	**0.092, 0.147**	**0.076, 0.131**	**0.129, 0.205**	**0.076, 0.149**	**0.025, 0.125**	**0.001, 0.069**	**0.091, 0.305**	**0.023, 0.128**
Flow								
Odds ratio	1.003	**0.997**	0.998	1.000	0.999	1.003	1.007	0.985
95% CI	0.998, 1.009	**0.995, 1.000**	0.996, 1.001	0.994, 1.005	0.980, 1.019	0.990, 1.017	0.985, 1.029	0.967, 1.004
Temperature								
Odds ratio	0.953	0.938	0.972	0.937	1.041	0.979	0.772	0.908
95% CI	0.800, 1.136	0.850, 1.034	0.887, 1.066	0.737, 1.190	0.898, 1.207	0.869, 1.102	0.549, 1.086	0.755, 1.092
Spill								
Odds ratio	**0.949**	0.978	0.982	0.984	0.898	0.950	0.859	1.185
95% CI	**0.915, 0.983**	0.934, 1.025	0.937, 1.028	0.926, 1.044	0.755, 1.069	0.805, 1.120	0.705, 1.046	0.867, 1.621
Salmon								
Odds ratio	1.010	1.024	**1.052**	1.043	**2.000**	1.320	1.000	**2.772**
95% CI	0.766, 1.330	0.985, 1.065	**1.017, 1.089**	0.989, 1.101	**1.094, 3.657**	0.757, 2.301	0.999, 1.001	**1.375, 5.585**
Shad								
Odds ratio	0.347	**0.997**	1.000	1.006	0.993	0.964	1.000	0.977
95% CI	0.064, 1.872	**0.994, 0.999**	0.997, 1.003	0.993, 1.019	0.951, 1.036	0.909, 1.024	1.000, 1.000	0.441, 2.166
Release site								
Odds ratio	NA	**1.776**	1.093	1.159	1.468	1.299	1.011	1.492
95% CI	—	**1.418, 2.223**	0.874, 1.367	0.885, 1.518	0.913, 2.362	0.796, 2.119	0.578, 1.766	0.808, 2.755
Fate								
Odds ratio	0.988	0.946	**2.210**	1.113	2.402	2.461	8.607	3.211
95% CI	0.759, 1.286	0.685, 1.307	**1.571, 3.110**	0.622, 1.993	0.575, 10.026	0.458, 13.22	0.387, 191.6	0.053, 195.4
Fate × Time								
Odds ratio	**1.304**	**1.475**	1.009	**2.054**	1.248	0.702	0.536	1.037
95% CI	**1.107, 1.535**	**1.074, 2.027**	0.939, 1.085	**1.181, 3.572**	0.473, 3.293	0.235, 2.091	0.138, 2.075	0.067, 16.100

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Table 1 (*continued*).

	Dam							
	Bonneville	The Dalles	John Day	McNary	Ice Harbor	Lower Monumental	Little Goose	Lower Granite
Sex								
Odds ratio	0.981	1.076	1.108	1.038	0.790	0.978	1.074	1.142
95% CI	0.872, 1.103	0.945, 1.225	0.972, 1.264	0.882, 1.220	0.589, 1.059	0.720, 1.329	0.766, 1.506	0.819, 1.592
Tag day								
Odds ratio	1.012	0.995	1.007	**1.017**	1.009	0.995	1.051	1.019
95% CI	0.991, 1.035	0.969, 1.021	0.990, 1.025	**1.004, 1.030**	0.985, 1.034	0.976, 1.016	0.950, 1.162	0.977, 1.062
Clipped								
Odds ratio	1.000	1.029	0.968	0.981	0.957	1.168	0.771	0.876
95% CI	0.884, 1.131	0.895, 1.183	0.839, 1.118	0.829, 1.160	0.709, 1.291	0.858, 1.589	0.532, 1.118	0.620, 1.239
Length								
Odds ratio	**0.987**	**0.986**	**0.986**	**0.985**	0.995	**0.976**	0.984	0.981
95% CI	**0.981, 0.993**	**0.980, 0.992**	**0.981, 0.992**	**0.978, 0.993**	0.973, 1.018	**0.959, 0.994**	0.964, 1.005	0.959, 1.004
Fall Chinook salmon								
N	2398	1535	1491	1222	231	146	104	63
Censored	186	145	205	107	42	13	6	6
% Censored	7.8	9.4	13.7	8.8	18.2	8.9	5.8	9.5
Unsuccessful	539	248	198	84	25	18	12	9
% Unsuccessful	22.5	16.2	13.3	6.9	10.8	12.3	11.5	14.3
Estimate								
TOD								
Odds ratio	**0.111**	**0.088**	**0.090**	**0.067**	**0.081**	**0.080**	**0.073**	**0.170**
95% CI	**0.093, 0.133**	**0.069, 0.111**	**0.070, 0.115**	**0.050, 0.089**	**0.041, 0.161**	**0.035, 0.185**	**0.027, 0.198**	**0.050, 0.577**
Flow								
Odds ratio	0.998	0.995	**0.995**	0.999	0.984	1.000	1.085	1.060
95% CI	0.995, 1.001	0.990, 1.000	**0.990, 1.000**	0.993, 1.004	0.921, 1.051	0.918, 1.090	0.956, 1.232	0.869, 1.295
Temperature								
Odds ratio	**1.076**	1.111	1.127	1.045	0.923	0.995	0.951	1.051
95% CI	**1.001, 1.157**	0.937, 1.318	0.980, 1.295	0.979, 1.116	0.725, 1.174	0.815, 1.214	0.743, 1.218	0.823, 1.342
Spill								
Odds ratio	NA	NA	NA	NA	NA	NA	NA	NA
95% CI	—	—	—	—	—	—	—	—
Salmon								
Odds ratio	1.009	1.008	1.012	1.005	1.016	1.008	1.000	**1.249**
95% CI	0.968, 1.052	0.990, 1.026	0.987, 1.037	0.986, 1.026	0.943, 1.096	0.914, 1.112	1.000, 1.000	**1.031, 1.513**
Shad								
Odds ratio	0.000	319.7	0.027	2.775	>10 000	0.000	1.174	0.000
95% CI	0.000, >10 000	0.022, >10 000	0.000, 265.8	0.011, 717.2	0.000, >10 000	0.000, >10 000	0.903, 1.526	0.000, >10 000
Release site								
Odds ratio	NA	1.194	1.041	0.990	1.493	0.937	1.764	0.444
95% CI	—	0.991, 1.439	0.861, 1.258	0.806, 1.216	0.947, 2.354	0.509, 1.722	0.693, 4.491	0.165, 1.193

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Table 1 (*continued*).

	Dam							
	Bonneville	The Dalles	John Day	McNary	Ice Harbor	Lower Monumental	Little Goose	Lower Granite
Fate								
Odds ratio	**1.562**	**1.511**	**2.100**	**2.254**	1.385	2.211	0.700	1.175
95% CI	**1.280, 1.905**	**1.242, 1.839**	**1.491, 2.959**	**1.552, 3.275**	0.653, 2.937	0.847, 5.771	0.175, 2.797	0.152, 9.070
Fate × Time								
Odds ratio	1.043	0.968	1.030	1.036	0.613	1.038	1.286	0.957
95% CI	0.999, 1.089	0.909, 1.031	0.983, 1.079	0.893, 1.202	0.295, 1.276	0.812, 1.326	0.348, 4.757	0.572, 1.603
Sex								
Odds ratio	0.990	1.099	0.995	1.013	1.264	0.985	1.154	0.592
95% CI	0.889, 1.103	0.958, 1.261	0.860, 1.150	0.867, 1.184	0.829, 1.925	0.600, 1.618	0.589, 2.261	0.234, 1.493
Tag day								
Odds ratio	0.995	1.013	1.011	0.996	1.016	0.991	1.031	1.000
95% CI	0.983, 1.006	0.992, 1.034	0.991, 1.032	0.984, 1.007	0.992, 1.042	0.964, 1.019	0.996, 1.067	0.946, 1.058
Clipped								
Odds ratio	1.147	1.007	1.008	0.732	1.261	0.682	0.356	0.282
95% CI	0.958, 1.375	0.790, 1.284	0.772, 1.315	0.561, 0.956	0.764, 2.082	0.348, 1.337	0.108, 1.180	0.047, 1.714
Length								
Odds ratio	0.995	**0.993**	0.993	0.995	**0.976**	0.989	0.950	0.978
95% CI	0.989, 1.000	**0.986, 1.000**	0.985, 1.000	0.987, 1.003	**0.954, 0.998**	0.962, 1.017	0.914, 0.986	0.933, 1.024
Steelhead (sea-run *Oncorhynchus mykiss*)								
N	3702	2972	2851	2029	2056	1583	1157	1179
Censored	174	88	246	227	142	48	59	73
% Censored	4.7	3.0	8.6	11.2	6.9	3.0	5.1	6.2
Unsuccessful	932	605	582	339	254	161	90	78
% Unsuccessful	25.2	20.4	20.4	16.7	12.4	10.2	7.8	6.6
Estimate								
TOD								
Odds ratio	**0.090**	**0.126**	**0.149**	**0.160**	**0.124**	**0.163**	**0.235**	**0.089**
95% CI	**0.077, 0.105**	**0.110, 0.144**	**0.131, 0.170**	**0.138, 0.185**	**0.106, 0.144**	**0.140, 0.191**	**0.201, 0.276**	**0.071, 0.112**
Flow								
Odds ratio	1.001	0.998	0.998	**0.997**	0.998	0.996	0.998	1.003
95% CI	0.997, 1.006	0.996, 1.000	0.995, 1.001	**0.993, 1.000**	0.979, 1.016	0.988, 1.003	0.986, 1.009	0.995, 1.012
Temperature								
Odds ratio	0.979	**0.962**	**1.035**	**1.061**	**1.066**	**1.043**	**1.043**	**1.049**
95% CI	0.936, 1.023	**0.935, 0.990**	**1.011, 1.059**	**1.021, 1.102**	**1.027, 1.106**	**1.023, 1.065**	**1.015, 1.071**	**1.022, 1.077**
Spill								
Odds ratio	0.974	1.008	0.958	1.007	**0.840**	0.924	0.836	1.050
95% CI	0.947, 1.001	0.965, 1.054	0.908, 1.011	0.941, 1.077	**0.761, 0.927**	0.588, 1.451	0.535, 1.306	0.837, 1.317
Salmon								
Odds ratio	1.002	**1.014**	**1.019**	1.023	1.046	1.023	**1.000**	**1.082**
95% CI	0.935, 1.074	**1.005, 1.023**	**1.002, 1.036**	0.987, 1.059	0.957, 1.143	0.979, 1.068	**1.000, 1.000**	**1.002, 1.168**

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Table 1 *(concluded).*

	Dam							
	Bonneville	The Dalles	John Day	McNary	Ice Harbor	Lower Monumental	Little Goose	Lower Granite
Shad								
Odds ratio	7.389	1.002	1.005	1.018	1.003	0.972	1.000	0.989
95% CI	0.793, 68.870	0.996, 1.007	0.998, 1.012	0.980, 1.059	0.942, 1.067	0.909, 1.039	1.000, 1.000	0.354, 2.759
Release site								
Odds ratio	NA	1.066	1.122	1.017	1.034	1.039	0.960	1.141
95% CI	—	0.950, 1.196	0.984, 1.278	0.879, 1.177	0.891, 1.201	0.883, 1.223	0.798, 1.155	0.917, 1.419
Fate								
Odds ratio	**1.182**	1.073	**1.347**	1.175	**1.405**	**1.333**	**1.817**	**2.226**
95% CI	**1.070, 1.305**	0.952, 1.208	**1.188, 1.526**	0.949, 1.454	**1.131, 1.746**	**1.016, 1.749**	**1.350, 2.445**	**1.543, 3.211**
Fate × Time								
Odds ratio	**1.049**	1.046	1.008	1.005	0.970	**1.259**	0.996	1.008
95% CI	**1.025, 1.074**	0.996, 1.099	1.000, 1.015	0.980, 1.030	0.926, 1.015	**1.075, 1.474**	0.964, 1.029	0.968, 1.049
Sex								
Odds ratio	1.052	**1.107**	1.057	1.024	1.051	1.026	1.079	1.053
95% CI	0.975, 1.136	**1.014, 1.207**	0.967, 1.155	0.913, 1.149	0.945, 1.170	0.912, 1.153	0.936, 1.244	0.915, 1.213
Tag day								
Odds ratio	**1.006**	**1.004**	1.001	**1.008**	**1.006**	1.003	1.004	1.004
95% CI	**1.003, 1.009**	**1.001, 1.007**	0.998, 1.004	**1.002, 1.013**	**1.001, 1.010**	0.997, 1.008	0.998, 1.009	0.996, 1.011
Clipped								
Odds ratio	1.035	1.017	1.006	1.032	0.985	1.020	1.045	0.929
95% CI	0.942, 1.139	0.916, 1.128	0.909, 1.114	0.900, 1.183	0.863, 1.124	0.886, 1.173	0.891, 1.226	0.784, 1.100
Length								
Odds ratio	1.002	0.997	**1.012**	0.998	1.002	1.006	1.003	1.003
95% CI	0.996, 1.009	0.990, 1.005	**1.006, 1.018**	0.989, 1.006	0.995, 1.009	0.998, 1.015	0.994, 1.012	0.994, 1.013

Notes: Odds ratios confidence intervals that do not include 1.0 are given in bold. Odds ratios estimate passage hazard (the probability of passage during any given time interval) for one group compared with another. Ratios are expressed as successful:unsuccessful, night:day, downstream:forebay, male:female, hatchery:wild. For example, odds ratios >1.0 for fate indicate a higher passage hazard (and lower passage time) for successful versus unsuccessful adults. Odds ratios for continuous predictor variables estimate change in hazard per unit increase in the predictor. Flow and spill are expressed as change in odds per 283 $m^3 \cdot s^{-1}$ (10 000 cubic feet per second), temperature as change in odds per °C, salmonids and shad as change per 10 000 fish in daily ladder count. TOD, time of day (night vs. day); shad, daily dam count of American shad (*Alosa sapidissima*); salmon, daily dam counts of all salmonids (*Oncorhynchus* spp.); NA, not applicable.

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not be directly estimated using PROC PHREG (Allison 1995, p. 160). This analytical limitation also prevented tests of year × fate interactions.

We used information-theoretic techniques (Burnham and Anderson 2002) to compare among the 15 potential models for each species–dam combination. Akiake's information criterion (AIC) and AIC weights (w_i) were used to identify the most parsimonious model(s), given the data. Model-averaging techniques were used to calculate model-averaged odds ratios and associated unconditional confidence intervals (CIs) that incorporate uncertainty about which model is best (Burnham and Anderson 2002). Details and results of model selection and averaging are given in Appendix S1[3]. We considered predictor variables to have explanatory power when the 95% CI of the odds ratio did not include 1.0.

On average, 6.7% (range: 1.3%–18.2%) of passage events had uncertain endpoints because of missing telemetry records at the fish ladder exit antenna. These passage events were censored from the analysis by removing them from the risk set at the time of last observation. Operational reasons for incomplete records included antenna outages or passage through an unmonitored navigational lock. Alternatively, individuals were censored because they entered a tailrace but did not pass the dam. We assigned censoring times using the last available record from antennas at the dam, and these were often at antennas near the ladder exit. We tested the effect of this criterion using the sensitivity analyses described below.

A critical assumption of time-event models is that censoring must not be informative with respect to treatment groups (Allison 1995; Hosmer and Lemeshow 1999). We observed that fish with unknown fates were more likely to be censored, violating this assumption (see Results). While the effect of informative censoring on model coefficients cannot be calculated (Allison 1995), the general effect can be assessed by performing sensitivity analyses where censoring times are assigned using different criteria and comparing the resulting estimated regression coefficients with those of the base model. If the coefficients do not change markedly, the effect of this violation on model conclusions is deemed small (Allison 1995). We used three alternative criteria in our analyses. First, we assumed that all censored fish would have passed immediately after the censoring time by including these fish as uncensored and using the censoring time as the time of ladder exit. Second, we assumed that all censored fish could have remained in the risk set until the end of observation by assigning censor times equal to the longest observed passage time. In a third analysis, we excluded a priori all fish that we did not observe to pass the dam under analysis to directly test for any delayed upstream effects of slow passage on fate among those fish that were known to have passed each dam.

Total passage time in the lower Columbia River hydrosystem

We were also interested in the relationship between migration performance and passage time past multiple dams. Specifically, we asked whether fish migration times through the lower Columbia River were longer for unsuccessful than for successful migrants, as observed in sockeye salmon (*Oncorhynchus nerka*) by Naughton et al. (2005). We used the analysis of variance (ANOVA) model $\log_e$(migration time) = year + fate + year × fate + error to test for differences in mean passage time by fate and year. Migration times for each fish were calculated between the first detection in the Bonneville tailrace to exit from a McNary fish ladder (four dams and three reservoirs). By definition, this analysis excluded forebay-released fish and any fish without a ladder exit record at McNary Dam. Passage times were $\log_e$-transformed to improve the normality of error terms. We also calculated the relative mean difference in passage time between fate classes for each year as $(\text{Time}_{\text{unsuccessful}} - \text{Time}_{\text{successful}})/\text{Time}_{\text{successful}}$ and then tested whether the mean difference among years differed significantly between fate classes using one-way ANOVA. All statistical analyses were performed in SAS v.9 PROC PHREG or GLM (SAS Institute Inc., Cary, North Carolina).

Results

Passage at individual dams

Most individual fish passed each dam rapidly, and median passage times at individual dams ranged from 0.2 to 2.7 days, depending on the species and year (Fig. 2). However, up to 57% of spring Chinook salmon took more than 2 days and as many as 32% took more than 5 days to pass individual dams each year. Summer and fall Chinook salmon passed more quickly than spring Chinook salmon, a pattern thought to be related to temperature effects on swimming speed (Brett 1995) and seasonal differences in discharge (Keefer et al. 2004*a*). Most steelhead passed during low-discharge conditions and also rapidly passed individual dams.

The results of PHReg multimodel selection using AIC revealed that the full model provided the best fit to the data in the majority of species–dam combinations, though in several cases there was considerable uncertainty about which model provided the best fit to the data (e.g., all model $w_i < 0.4$, Supplemental Appendix S1[3]). Nonetheless, model coefficients remained nearly identical among models (Supplemental Appendix S1[3]). There were important differences among years in passage behavior that appeared to be primarily related to annual variation in mean river flow. Though we were unable to directly assess the effects of interannual variation on passage hazard, models not stratified by year had the worst AIC score in all cases (Supplemental Appendix S1[3]).

Several environmental predictors provided explanatory power for one or more runs within year. Odds ratios compared the probability of passage between categories within any given time interval, or the change in odds as predictor variables increased by one unit. Time of day was the strongest and most consistent effect within year across all runs and dams because few fish passed at night. Individual fish were one-fifth to less than one-twentieth as likely to pass during night as day (Table 1). When different from even, odds ratios for flow were always less than 1.0 and indicated a 0.2%–0.67% decrease in the instantaneous probability of passage per 283 $m^3 \cdot s^{-1}$ (10 000 cubic feet per second) increase of flow. Spill had a similar, but stronger effect, with passage hazard decreasing 5.1%–22.1% per 283 $m^3 \cdot s^{-1}$. Increasing temperature was generally associated with faster

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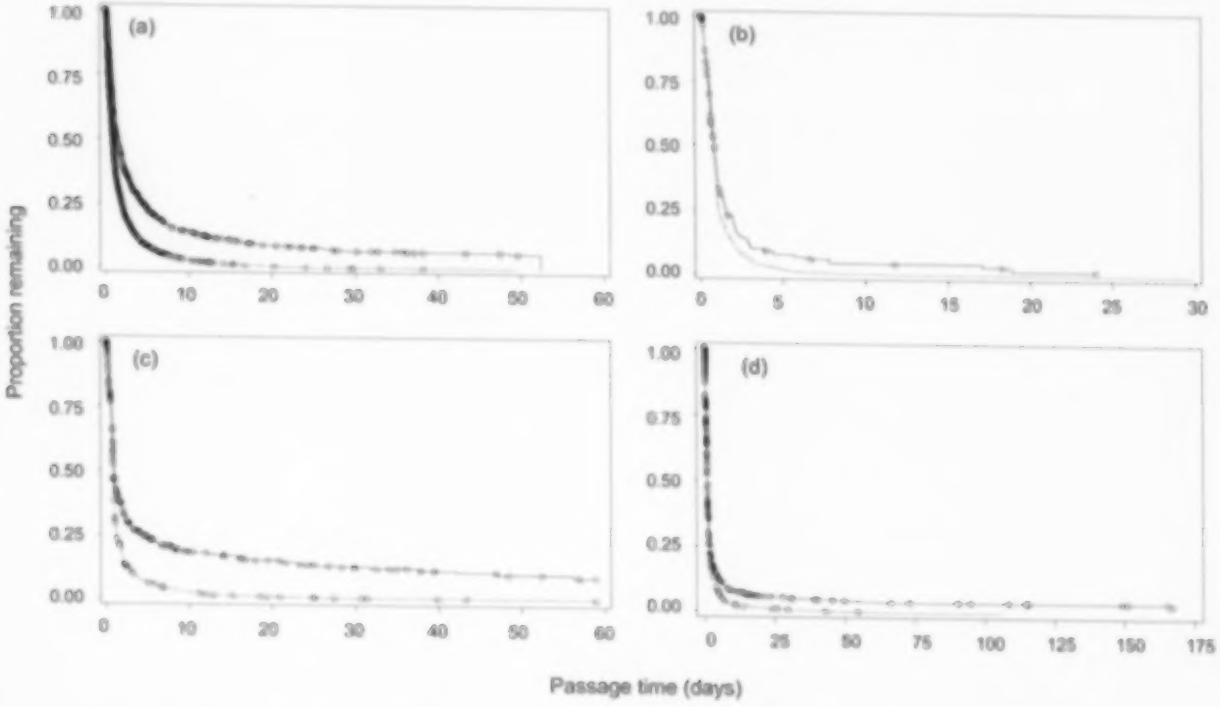
Fig. 2. Inverse cumulative passage time curves for each run analyzed by fate, all years and dams combined: (*a*) spring Chinook salmon (*Oncorhynchus tshawytscha*), (*b*) summer Chinook salmon, (*c*) fall Chinook salmon, and (*d*) steelhead (sea-run *Oncorhynchus mykiss*). Note differences in time scale. The passage time curves for unsuccessful migrants are depicted with solid lines; successful migrants are shown with broken lines. Censoring times for individual adults are indicated by open circles.



passage, particularly for spring Chinook salmon, which pass prior to the onset of stressful temperature conditions (e.g., ≤18 °C; Table 1). Odds ratios for date of tagging indicated that passage hazard increased 0.4–5.1%·day^{-1} within year during the run. This pattern is consistent with other findings that individuals migrating late within runs tend to migrate faster, presumably to reach spawning grounds during the appropriate spawning period (e.g., Quinn and Adams 1996; McLean et al. 2004). In some cases, the number of salmonids present in the ladder was positively associated with passage hazard, revealing that higher densities of adult salmonids within ladders did not slow individual passage. Conversely, at the lower Columbia River dams where large numbers of American shad pass, passage hazards were negatively associated with shad numbers for spring Chinook salmon at all dams except Bonneville Dam. Passage hazard frequently decreased with increasing fish size in the Chinook salmon runs and was not consistently related to sex. Fish released downstream from Bonneville Dam passed more rapidly at The Dalles and John Day dams than those released to the Bonneville Dam forebay for most runs. There was no consistent association between fish origin (hatchery vs. wild) and passage hazard.

The time-event analyses were primarily structured to test for an association between passage time and eventual migration to spawning sites, while statistically controlling for the effects of environmental variables and fish traits. Fate was associated with passage hazard or there was a significant interaction between fate and passage hazard for 22 out of 24 (91.7%) of dam and run combinations, excluding summer and fall Chinook salmon at Snake River dams, where samples sizes were small ($N_{unsuccessful} < 25$; Table 1). The odds ratio for fate ranged from 1.347 to 2.254 in 11 cases where there was no significant interaction between fate and passage time, indicating that eventually successful fish were 34.7%–225.4% more likely than unsuccessful fish to pass during any given time interval. In one-half of the dam–run combinations (12 of 24, excluding the small samples at Snake River dams), there was a significant fate × passage time interaction. In all cases, odds ratios were greater than 1.0, indicating that successful fish became increasingly more likely to pass during any given interval as the time since tailrace detection increased compared with unsuccessful fish.

Fish that were eventually unsuccessful were censored significantly more frequently than successful fish in all four runs (Supplemental Appendix S2[3]), violating an assumption of the Cox proportional hazard regression. The results of three sensitivity analyses differing in their handling of censored fish suggested this violation did not seriously bias the PHReg parameters nor provide false evidence of a relationship between passage time and fate (Supplemental Appendix S2[3]).

Total passage time through the lower Columbia River hydrosystem

Among Chinook salmon, summer Chinook were fastest

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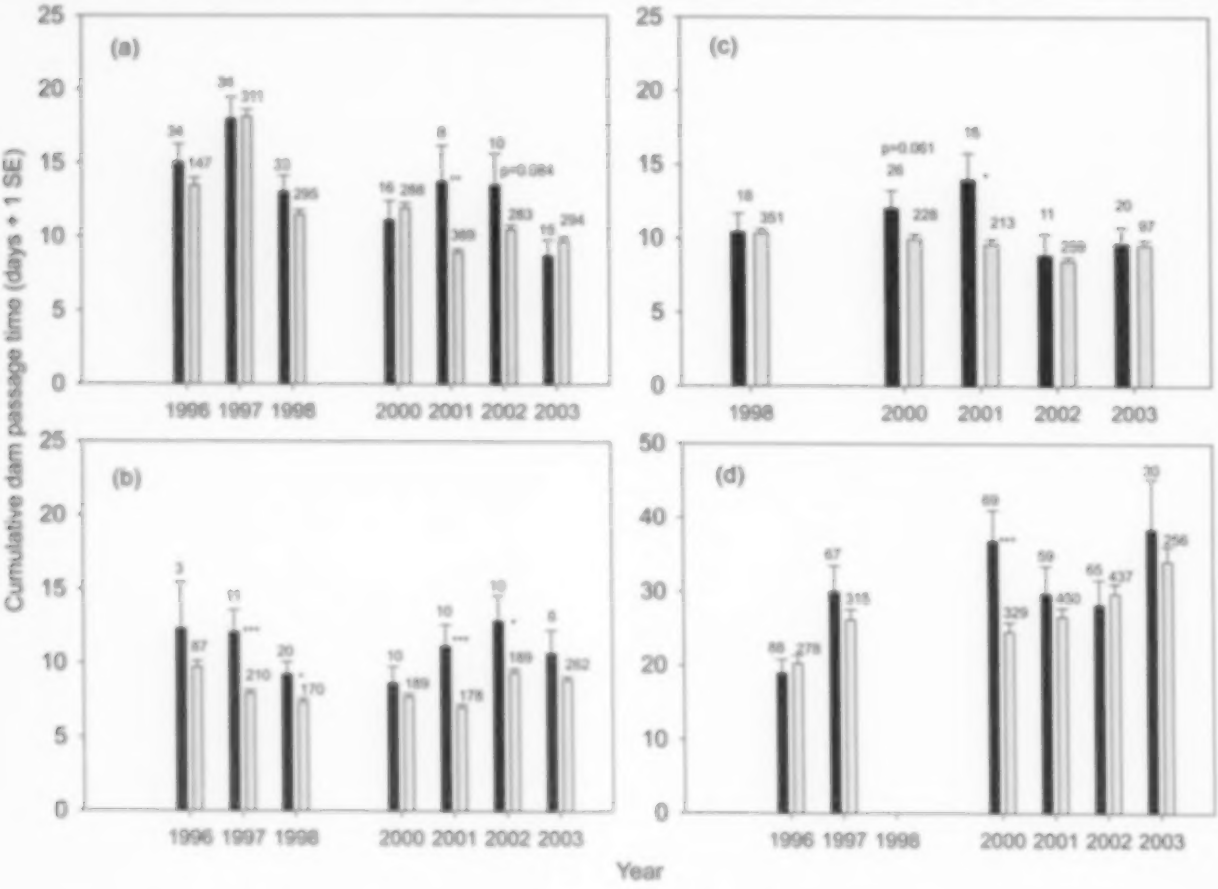
Fig. 3. Mean passage time by fate for each species and year: (*a*) spring Chinook salmon (*Oncorhynchus tshawytscha*), (*b*) summer Chinook salmon, (*c*) fall Chinook salmon, and (*d*) steelhead (sea-run *Oncorhynchus mykiss*). Unsuccessful adults are indicated by solid bars; successful adults are shown by shaded bars. Note the difference in the y axis for steelhead; passage times were approximately two times longer than Chinook salmon passage times. Sample sizes given above each bar. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.



and spring Chinook had the slowest passage times through the lower Columbia River hydrosystem. In contrast with passage times at individual dams, steelhead passage times through the lower Columbia River hydrosystem were approximately double those for Chinook salmon (Fig. 3), reflecting extended temporary straying by steelhead into cooler tributaries during the warmest months (see Keefer et al. 2004*a* and High et al. 2006 for more details).

Averaged across all years, mean passage times from the Bonneville tailrace to the McNary Dam forebay (235 rkm and four dams) were faster for successful migrants than for unsuccessful migrants that passed McNary Dam but did not reach spawning tributaries (spring Chinook salmon: $F_{[13.2125]} = 41.73$, $P_{fate} = 0.0190$, $P_{year} < 0.0001$, $P_{fate \times year} = 0.0655$; summer Chinook salmon: $F_{[13.1348]} = 10.42$, $P_{fate} < 0.0001$, P_{year} 0.0015, $P_{fate \times year} = 0.4059$; fall Chinook salmon: $F_{[9.1329]} = 4.64$, $P_{fate} = 0.0231$, P_{year} 0.0198, $P_{fate \times year} = 0.1657$; steelhead: $F_{[11.2433]} = 7.43$, $P_{fate} = 0.0451$, $P_{year} < 0.0001$, $P_{fate \times year} = 0.0645$; Fig. 3). The observed point estimates for differences between fate groups varied from year to year in all runs except summer Chinook salmon, with some weak evidence of a fate × year interaction in spring Chinook salmon and steelhead ($P \leq 0.0655$). The mean annual relative difference in lower Columbia River passage time between fate categories was also significant for all four runs, with unsuccessful passage times 4.2%–16.1% longer than those for eventually successful migrants ($0.0001 < P \leq 0.0451$; Supplemental Appendix S3[1]). These estimates may have underestimated the true differences in passage time between fate groups because unsuccessful adults not passing McNary Dam could not be included in the analysis.

Discussion

The migration success of adult Chinook salmon and steelhead was inversely related to passage time through the dams and reservoirs of the Columbia River hydrosystem, according to our detailed analysis of radiotelemetric data. We observed that the majority of adult salmonids rapidly passed as many as eight dams and successfully reached their natal spawning sites. However, many fish required more than 2 days to pass individual dams, some took several weeks to

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pass, and some did not pass at all. Adults with unknown fates — those that were not detected at spawning sites after passing one or more dams — had consistently longer passage times at individual dams and through a multidam reach of the lower Columbia River. These patterns are striking, but cannot demonstrate an underlying mechanism(s), nor do the relationships reveal the relative importance of dams versus other factors in reducing the migration success of slow adults. However, the patterns in passage time do suggest several potential mechanisms that may have contributed to the observed relationships.

Passage environment and fish traits

Within season, passage hazards were related to time of day, flow, spill, water temperature, densities of adult fishes in ladders, and fish length. The single strongest predictor was time of day, because salmonids infrequently pass dams at night (Naughton et al. 2005). Slower passage at high flows probably reflected both decreased ground speed of fish swimming through higher velocity water (e.g., Hinch and Rand 1998) and an increase in the searching time required to find fishway entrances in a more turbulent tailrace environment. Water was passed over dam spillways during spring and summer in most years, dramatically increasing turbulence in tailraces and potentially accounting for the stronger association of passage hazard with spill than with flow. Detailed analyses of an experiment that manipulated spill levels in the lower Columbia River during 2000–2003 were consistent with those reported here (Caudill et al. 2006*a*).

Water temperature has dramatic effects on salmon physiology and behavior (Brett 1995). Cool, early spring temperatures (5–8 °C) compared with near optimal late spring temperatures (~15–17 °C; Brett 1995; Salinger and Anderson 2006) probably explain the positive association between temperature and passage hazard for spring Chinook salmon at lower Columbia River dams. Fall Chinook salmon and steelhead encounter warm, and in some cases stressful, temperatures (18–23 °C; Richter and Kolmes 2005) during August and early September and then cooler temperatures as the run season progresses.

The consistent, negative relationship between body length and passage hazard was somewhat surprising because optimal swimming speed increases with body size (Brett 1995). However, the factors influencing optimum swim speed, migration efficiency, and body size are complex (Hinch and Rand 1998; Crossin et al. 2004*a*; Hughes 2004). Indeed, interpopulation patterns of body size suggest selection for smaller size in long-distance migrating stocks (reviewed in Quinn 2005), though how this would relate to swim speed measured over smaller scales remains unclear. Clearly, the study of the relationships among temperature, body size, swimming speed, and river environment deserves further study.

Interestingly, passage hazards increased, corresponding to shorter passage times, as the number of concurrently passing adult salmonids increased in some models, particularly for Snake River spring Chinook salmon. This result provides no evidence for negative, density-dependent effects and may have resulted from the fact that the peak run presumably occurs during the period of optimal migration conditions, resulting in large numbers of fish moving quickly compared with early or late in the run. Conversely, the number of American shad was negatively associated with passage hazard in spring Chinook salmon at three out of four lower Columbia River dams. This result suggests the potential for high densities of American shad to slow the migration of salmonids, but could be related to the fact that shad only begin passing Bonneville Dam after most spring Chinook salmon have passed (DART 2005).

Potential underlying mechanisms affecting the passage time – fate relationship

An important question is whether the passage time – fate relationship was caused by impoundment or whether the pattern was primarily related to the rigors of long-distance migration and would have been observed in the unmodified system. In the transformed Columbia–Snake hydrosystem, rapid passage of low-velocity reservoirs appears to compensate for relative slow passage through high-velocity tailraces and over dams (Keefer et al. 2004*a*; Naughton et al. 2005). Temperature conditions appear to be elevated in the modified system because of the effects of regional climate warming, changing land- and water-use patterns, and the direct effects of impoundment (Quinn and Adams 1996; Quinn et al. 1997), potentially increasing the metabolic costs of migration. Spill frequently elevates dissolved gas levels above saturation and can cause gas bubble disease at extreme supersaturation levels (Johnson et al. 2005), and high spill levels are associated with slowed passage (Caudill et al. 2006*a*). In constrast, impoundment may reduce migration costs by reducing peak spring flows and because current fish passage facilities may be less challenging in terms of velocity barriers than the cascades and rapids of the predam migration corridor. Historically, migration up the lower Columbia River included dramatic obstacles, such as Cascade Rapids and the 6 m high Celilo Falls, which are both now inundated. Below, we outline four causal mechanisms that may have contributed to the observed passage time – fate relationship.

First, environmental conditions during migration probably contributed to the passage time – fate relationship. Factors that increase the time spent in dam tailraces and fishways, including high spill and flow levels (Caudill et al. 2006*a*), fallback behavior (Boggs et al. 2004), temperature (Caudill et al. 2006*b*; Goniea et al. 2006; High et al. 2006), and hydraulics at the base of ladders (Naughton et al. 2006), may be particularly important to the overall energetics of migration and migration success because passage of these areas is energetically demanding (Brown and Geist 2002; Brown et al. 2006). Generally, impoundment, hydrosystem operations, and natural climate drivers affect the environmental conditions encountered by migrating fishes in regulated rivers in ways that probably influence migration success, including in this study. The analysis of passage time data using the PHReg approach provides powerful, dynamic statistical control of measured environmental variation when comparing fate classes, though we note that additional, unmeasured environmental variation in this study that affected both passage time and fate may have contributed to the observed patterns.

Second, variation in passage behavior among individuals may have contributed to the observed passage time – fate relationship. Individual responses to complex hydraulic, tem-

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perature, light, olfactory, and other cues during migration are variable (Standen et al. 2004; Caudill et al. 2006*b*; Keefer et al. 2006). Hinch and Bratty (2000) observed that some sockeye salmon adults exhibited nonoptimal rapid swimming behaviors in high-flow, turbulent areas at Hell's Gate on the Fraser River. Rapid swimming was also associated with unsuccessful passage. Thus, the long passage times and unsuccessful migration of some adults may have been caused by inefficient responses to the passage conditions encountered at dams. Whether relatively slow passage and unsuccessful migration were caused by the artificial conditions at dams or reflect underlying natural variation in behavior remains unknown.

Third, the relationship may represent selection for physiological and locomotory traits needed to traverse velocity barriers at natural falls and artificial channel constrictions. Passage of such velocity barriers is physiologically demanding (Hinch and Rand 1998; Hinch and Bratty 2000; Standen et al. 2002), slowing the upstream migration of fishes in the Columbia–Snake hydrosystem (Williams 1998; Keefer et al. 2004*a*) and in other salmonid (Karppinen et al. 2002; Laine et al. 2002) and non-salmonid fishes (e.g., Moser et al. 2002*a*; Zigler et al. 2004). Such barriers may be impassable depending on species and individual fish traits and condition (Moser et al. 2002*b*; Haro et al. 2004; Reiser et al. 2006). Under this mechanism, relatively weak swimmers would require greater periods to pass individual dams and also be less likely to successfully pass other velocity barriers upstream, including other dams.

Fourth, the relationship may have resulted from variation among individuals in energetic and (or) physiological condition upon river entry, which is determined largely by growth and development in the ocean. Individual salmon differ considerably in total energy content or density upon river entry both within (Pinson 2005) and among years (Crossin et al. 2004*b*). Adults in poor initial condition, especially those with relatively low energy content, may travel more slowly through high-gradient reaches and be less likely to complete migration. Young et al. (2006) found that among late-run Fraser River sockeye salmon entering fresh water abnormally early, unsuccessful migrants had lower gross somatic energy, higher plasma lactate (indicating recent anaerobic respiration), and higher levels of reproductive hormones, suggesting that unsuccessful individuals had a smaller initial energetic buffer against stress.

Notably, there is potential for these mechanisms to interact. Relatively slow migration past any project could deplete energy reserves, potentially alter subsequent fish behavior and orientation ability, reduce the ability to ascend ladders and traverse velocity barriers, and thereby increase the potential for further slowed and (or) failed migration at upstream dams. Poor initial condition (Crossin et al. 2004*a*) and (or) environmental conditions (Rand and Hinch 1998) during migration could further increase the probability of a fish entering this cycle. Ocean conditions prior to river entry were considered relatively good during the study period (e.g., Scheuerell and Williams 2005), suggesting reduced migration success and perhaps higher odds ratios for the passage time – fate relationship following a downturn in ocean conditions.

We were able to assess migration success to spawning tributaries and note that relatively slow migration in the hydrosystem may have reduced reproductive success on spawning grounds as well. Migration experience can influence reproductive success (e.g., Patterson et al. 2004), adults with longer migration times consume a greater proportion of energy reserves to reach spawning tributaries (Pinson 2005), and adults may hold for periods of weeks to months prior to spawning. Consequently, low initial energetic content and energetic depletion during migration have been implicated as a contributing factor for prespawn mortality in tributaries (Gilhousen 1990; Cooke et al. 2004; Pinson 2005), an area of increasing concern given high prespawn mortality rates observed in some sockeye and Chinook salmon populations in recent years (Cooke et al. 2004; Pinson 2005).

These results represent one of the first large-scale examinations of the relationship between migration behavior and fate in an anadromous fish. Anadromous and catadromous fishes are thought to be particularly vulnerable to human-induced environmental change because they must have suitable migration corridors in addition to suitable breeding, growth, and (or) overwintering–holding habitats, and because river systems worldwide have been strongly altered by damming and other human activities (Postel and Richter 2003). Long-distance migrating stocks, such as the interior salmonid stocks studied here, may be at particular risk given the relatively high cost of migration, low reserves upon reaching spawning sites, long prespawn holding periods, and marginal thermal regime encountered during migration by some migrants. Clearly, the successful management of habitats for long-distance migrants, especially diadromous fishes, will require mechanistic knowledge of how initial traits and condition, migration behavior, and environmental conditions interact to determine migration performance and reproductive success. The results also illustrate the importance of assessing the indirect effects of dams, including delayed or carry-over effects, because successful completion of migration was clearly associated with passage times and behaviors at downstream dams. Because of logistical and monetary constraints, the vast majority of studies examining the effects of dams on fishes has been conducted at local scales and has focused on short-term phenomena such as behavior at passage structures (i.e., survival past an individual project). Efforts should be made to increase the use of fitness-based performance measures, rather than behavioral or short-term survival criteria, for setting standards for passage facilities and in-river conditions, because long-term population viability ultimately rests on mean fitness remaining at or above replacement.

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References

Allison, P.D. 1995. Survival analysis using SAS: a practical guide. SAS Institute Inc., Cary, N.C.

Bell, M.C. 1991. Fisheries handbook of engineering requirements and biological criteria. US Army Corps of Engineers, North Pacific Division, Portland, Ore.

Boggs, C.T., Keefer, M.L., Peery, C.A., and Bjornn, T.C. 2004. Fallback, reascension, and adjusted fishway escapement estimates for adult chinook salmon and steelhead at Columbia and Snake River dams. Trans. Am. Fish. Soc. **133**: 932–949.

Brett, J.R. 1995. Energetics. *In* Physiological ecology of Pacific salmon. *Edited by* C. Grott, L. Margolis, and W. Clarke. University of British Columbia Press, Vancouver, B.C. pp. 3–68.

Brown, R.S., and Geist, D.R. 2002. Determination of swimming speeds and energetic demands of upriver migrating fall chinook salmon (*Oncorhynchus tshawytscha*) in the Klickitat River. Report of Pacific Northwest National Laboratory to Bonneville Power Administration, Portland, Ore. Proj. No. 22063.

Brown, R.S., Geist, D.L., and Mesa, M.G. 2006. Use of electromyogram telemetry to assess swimming activity of adult spring Chinook salmon migrating past a Columbia River dam. Trans. Am. Fish. Soc. **135**: 281–287.

Bunt, C.M., van Poorten, B.T., and Wong, L. 2001. Denil fishway utilization patterns and passage of several warmwater species relative to seasonal, thermal and hydraulic dynamics. Ecol. Freshw. Fish, **10**(4): 212–219.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.

Castro-Santos, T., and Haro, A. 2003. Quantifying migratory delay: a new application of survival analysis methods. Can. J. Fish. Aquat. Sci. **60**(8): 986–996.

Caudill, C.C., Peery, C.A., Daigle, W.R., Jepson, M.A., Boggs, C.T., Bjornn, T.C., and Joosten, D. 2006*a*. Adult Chinook salmon and steelhead dam passage behavior in response to manipulated discharge through spillways at Bonneville Dam. Report for US Army Corps of Engineers, Portland District, Portland, Ore.

Caudill, C.C., Clabough, T.S., Naughton, G.P., Peery, C.A., and Burke, B.J. 2006*b*. Water temperatures in adult fishways at mainstem dams on the Snake and Columbia Rivers. Phase 2. Biological effects. Report for US Army Corps of Engineers, Walla Walla District, Walla Walla, Wash.

Clay, C.H. 1995. Design of fishways and other fish facilities, second edition. Lewis Publishers, Boca Raton, Fla.

Cooke, S.J., Hinch, S.G., Farrell, A.P., Lapointe, M.F., Jones, S.R.M., Macdonald, J.S., Patterson, D.A., Healey, M.C., and Van Der Kraak, G. 2004. Abnormal migration timing and high en route mortality of sockeye salmon in the Fraser River, British Columbia. Fisheries, **29**(2): 22–33.

Crossin, G.T., Hinch, S.G., Farrell, A.P., Higgs, D.A., Lotto, A.G., Oakes, J.D., and Healey, M.C. 2004*a*. Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. J. Fish. Biol. **65**(3): 788–810.

Crossin, G.T., Hinch, S.G., Farrell, A.P., Higgs, D.A., and Healey, M.C. 2004*b*. Somatic energy of sockeye salmon *Oncorhynchus nerka* at the onset of upriver migration: a comparison among ocean climate regimes. Fish. Oceanogr. **13**(5): 345–349.

DART (Data Access in Real Time). 2005. Columbia River data access in real time [online]. Available from www.cbr.washington.edu/dart/dart.html [accessed June 2005; updated 13 April 2007].

Dudgeon, D. 2003. The contribution of scientific information to the conservation and management of freshwater biodiversity in tropical Asia. Hydrobiologia, **500**: 295–314.

Geist, D.R., Abernethy, C.S., Blanton, S.L., and Cullinan, V.I. 2000. The use of electromyogram telemetry to estimate energy expenditure of adult fall chinook salmon. Trans. Am. Fish. Soc. **129**(1): 126–135.

Gilhousen, P. 1990. Prespawning mortalities of sockeye salmon in the Fraser River system and possible causal factors. Int. Pac. Salmon Fish. Comm. Bull. 26.

Goniea, T.M., Keefer, M.L., Bjornn, T.C., Peery, C.A., Bennett, D.H., and Stuehrenberg, L.C. 2006. Behavioral thermoregulation and slowed migration by adult fall Chinook salmon in response to high Columbia River water temperatures. Trans. Am. Fish. Soc. **135**: 408–419.

Haro, A., and Kynard, B. 1997. Video evaluation of passage efficiency of American shad and sea lamprey in a modified Ice Harbor fishway. N. Am. J. Fish. Manag. **17**: 981–987.

Haro, A., Castro-Santos, T., Noreika, J., and Odeh, M. 2004. Swimming performance of upstream migrant fishes in open-channel flow: a new approach to predicting passage through velocity barriers. Can. J. Fish. Aquat. Sci. **61**(9): 1590–1601.

Hart, D.D., and Poff, N.L. 2002. A special section on dam removal and river restoration. Bioscience, **52**(8): 653–655.

High, B., Peery, C.A., and Bennett, D.H. 2006. Temporary straying of Columbia River summer steelhead in coolwater areas and its effect on migration rates. Trans. Am. Fish. Soc. **135**: 519–528.

Hinch, S.G., and Bratty, J. 2000. Effects of swim speed and activity pattern on success of adult sockeye salmon migration through an area of difficult passage. Trans. Am. Fish. Soc. **129**(2): 598–606.

Hinch, S.G., and Rand, P.S. 1998. Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): role of local environment and fish characteristics. Can. J. Fish. Aquat. Sci. **55**(8): 1821–1831.

Hosmer, D., Jr., and Lemeshow, S. 1999. Applied survival analysis: regression modeling of time to event data. Wiley Interscience, New York.

Hughes, N.F. 2004. The wave-drag hypothesis: an explanation for size-based lateral segregation during the upstream migration of salmonids. Can. J. Fish. Aquat. Sci. **61**(1): 103–109.

Johnson, E.L., Clabough, T.S., Bennett, D.H., Bjornn, T.C., Peery, C.A., Caudill, C.C., and Stuehrenberg, L.C. 2005. Migration depths of adult spring and summer chinook salmon in the lower Columbia and Snake Rivers in relation to dissolved gas supersaturation. Trans. Am. Fish. Soc. **134**(5): 1213–1227.

Karppinen, P., Makinen, T.S., Erkinaro, J., Kostin, V.V., Sadkovskij, R.V., Lupandin, A.I., and Kaukoranta, M. 2002. Migratory and route-seeking behaviour of ascending Atlantic salmon in the regulated River Tuloma. Hydrobiology, **483**(1–3): 23–30.

Keefer, M.L., Peery, C.A., Bjornn, T.C., Jepson, M.A., and Stuehrenberg, L.C. 2004*a*. Hydrosystem, dam, and reservoir

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passage rates of adult chinook salmon and steelhead in the Columbia and Snake Rivers. Trans. Am. Fish. Soc. **133**(6): 1413–1439.

Keefer, M.L., Peery, C.A., Jepson, M.A., Tolotti, K.R., Bjornn, T.C., and Stuehrenberg, L.C. 2004*b*. Stock-specific migration timing of adult spring–summer chinook salmon in the Columbia River basin. N. Am. J. Fish. Manag. **24**(4): 1145–1162.

Keefer, Peery, M.L., C.A., Jepson, M.A., and Stuehrenberg, L.C. 2004*c*. Upstream migration rates of radio-tagged adult chinook salmon in riverine habitats of the Columbia River basin. J. Fish Biol. **65**(4): 1126–1141.

Keefer, M.L., Peery, C.A., Ringe, R.R., and Bjornn, T.C. 2004*d*. Regurgitation rates of intragastric radio transmitters by adult chinook salmon and steelhead during upstream migration in the Columbia and Snake Rivers. N. Am. J. Fish. Manag. **24**(1): 47–54.

Keefer, M.L., Peery, C.A., Daigle, W.R., Jepson, M.A., Lee, S.R., Boggs, C.T., Tolotti, K.R., and Burke, B.A. 2005. Escapement, harvest, and unknown loss of radio-tagged adult salmonids in the Columbia River – Snake River hydrosystem. Can. J. Fish. Aquat. Sci. **62**: 930–949.

Keefer, M.L., Caudill, C.C., Peery, C.A., and Bjornn, T.C. 2006. Route selection in a large river during the homing migration of Chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **63**: 1752–1762.

Laine, A., Jokivirta, T., and Katopodis, C. 2002. Atlantic salmon, *Salmo salar* L., and sea trout, *Salmo trutta* L., passage in a regulated northern river — fishway efficiency, fish entrance and environmental factors. Fish. Manag. Ecol. **9**(2): 65–77.

Lucas, M., and Frear, P. 1997. Effects of a flow-gauging weir on the migratory behvaior of adult barbel, a riverine cyprinid. J. Fish Biol. **50**: 382–396.

McLean, J.E., Bentzen, P., and Quinn, T.P. 2004. Does size matter? Fitness-related factors in steelhead trout determined by genetic parentage assignment. Ecology, **85**(11): 2979–2985.

Monk, B., Weaver, D., Thompson, C., and Ossiander, F. 1989. Effects of flow and weir design on the passage behavior of American shad and salmonids in an experimental fish ladder. N. Am. J. Fish. Manag. **9**: 60–67.

Moser, M.L., Durazsdi, A.M., and Hall, J.R. 2000. Improving passage efficiency of adult American shad at low-elevation dams with navigation locks. N. Am. J. Fish. Manag. **20**(2): 376–385.

Moser, M.L., Ocker, P.A., Stuehrenberg, L.C., and Bjornn, T.C. 2002*a*. Passage efficiency of adult pacific lampreys at hydropower dams on the lower Columbia River, USA. Trans. Am. Fish. Soc. **131**(5): 956–965.

Moser, M.L., Matter, A.L., Stuehrenberg, L.C., and Bjornn, T.C. 2002*b*. Use of an extensive radio receiver network to document Pacific lamprey (*Lampetra tridentata*) entrance efficiency at fishways in the Lower Columbia River, USA. Hydrobiology, **483**(1–3): 45–53.

Moser, M.L., Zabel, R.W., Burke, B.A., Struehrenberg, L.C., and Bjornn, T.C. 2005. Factors affecting adult Pacific lamprey passage rates at hydropower dams: using "time to event" analysis of radiotelemetry data. *In* Aquatic Telemetry: Advances and Applications. Proceedings of the Fifth Conference on Fish Telemetry, 9–13 June 2003, Ustica, Italy. *Edited by* M.T. Spedicato, G. Lembo and G. Marmulla. FAO-COISPA, Rome. pp. 61–70.

Naughton, G.P., Caudill, C.C., Keefer, M.L., Bjornn, T.C., and Struehrenberg, L.C. 2005. Late-season mortality during migration of radio-tagged adult sockeye salmon (*Onchorhynchus nerka*) in the Columbia River. Can. J. Fish. Aquat. Sci. **62**: 30–47.

Naughton, G.P., Caudill, C.C., Peery, C.A., Clabough, T.S., Jepson, M.A., Bjornn, T.C., and Stuehrenberg, L.C. 2006. Experimental evaluation of fishway modifications on the passage behavior of adult Chinook salmon and steelhead at Lower Granite Dam, Snake River, USA. River Res. Appl. **23**: 99–111.

Northcote, T.G. 1998. Migratory behaviour of fish and its significance to movement through riverine fish passage facilities. *In* Fish migration and fish bypass. *Edited by* M. Jungwirth, S. Schmutz, and S. Weiss. Fishing News Books, Oxford. pp. 3–18.

NRC (National Research Council). 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, D.C.

Patterson, D.A., Macdonald, J.S., Hinch, S.G., Healey, M.C., and Farrell, A.P. 2004. The effect of exercise and captivity on energy partitioning, reproductive maturation and fertilization success in adult sockeye salmon. J. Fish Biol. **64**(4): 1039–1059.

Pinson, A. 2005. Energy use, migration time, and spawning success of adult chinook salmon returning to the South Fork Salmon River in Central Idaho. M.Sc. thesis, Department of Fish and Wildlife Resources, University of Idaho, Moscow, Idaho.

Poff, N.L., and Hart, D.D. 2002. How dams vary and why it matters for the emerging science of dam removal. Bioscience, **52**(8): 659–668.

Postel, S., and Richter, B. 2003. Rivers for life: managing water for people and nature. Island Press, Washington, D.C.

Quinn, T.P. 2005. The behavior and ecology of Pacific salmon. American Fisheries Society, Bethesda, Md.

Quinn, T.P., and Adams, D.J. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. Ecology, **77**(4): 1151–1162.

Quinn, T.P., Hodgson, S., and Peven, C. 1997. Temperature, flow, and the migration of adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. Can. J. Fish. Aquat. Sci. **54**(6): 1349–1360.

Rand, P.S., and Hinch, S.G. 1998. Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): simulating metabolic power and assessing risk of energy depletion. Can. J. Fish. Aquat. Sci. **55**(8): 1832–1841.

Reischel, T.S., and Bjornn, T.C. 2003. Influence of fishway placement on fallback of adult salmon at the Bonneville Dam on the Columbia River. N. Am. J. Fish. Manag. **23**(4): 1215–1224.

Reiser, D.W., Huang, C.M., Beck, S., Gagner, M., and Jeanes, E. 2006. Defining flow windows for upstream passage of adult anadromous salmonids at cascades and falls. Trans. Am. Fish. Soc. **135**(3): 668–679.

Richter, A., and Kolmes, S.A. 2005. Maximum temperature limits for chinook, coho, and chum salmon, and steelhead trout in the Pacific Northwest. Rev. Fish. Sci. **13**(1): 23–49.

Ruckelshaus, M.H., Levin, P., Johnson, J.B., and Kareiva, P.M. 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. Annu. Rev. Ecol. Syst. **33**: 665–706.

Salinger, D.H., and Anderson, J.J. 2006. Effects of water temperature and flow on adult salmon migration swim speed and delay. Trans. Am. Fish. Soc. **135**: 188–199.

Scheuerell, M.D., and Williams, J.G. 2005. Forecasting climate-induced changes in the survival of Snake River spring/summer Chinook salmon *Oncorhynchus tshawytscha*. Fish. Oceanogr. **14**(6): 448–457.

Standen, E.M., Hinch, S.G., Healey, M.C., and Farrell, A.P. 2002. Energetic costs of migration through the Fraser River Canyon, British Columbia, in adult pink (*Oncorhynchus gorbuscha*) and sockeye (*Oncorhynchus nerka*) salmon as assessed by EMG telemetry. Can. J. Fish. Aquat. Sci. **59**(11): 1809–1818.

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Standen, E.M., Hinch, S.G., and Rand, P.S. 2004. Influence of river speed on path selection by migrating adult sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **61**(6): 905–912.

Williams, J.G. 1998. Fish passage in the Columbia River, USA and its tributaries: problems and solutions. *In* Fish migration and fish bypass. *Edited by* M. Jungwirth, S. Schmutz, and S. Weiss. Fishing News Books, Oxford. pp. 180–191.

Young, J.L., Hinch, S.G., Cooke, S.J., Crossin, G.T., Patterson, D.A., Farrell, A.P., Van Der Kraak, G., Lotto, A.G., Lister, A., Healey, M.C., and English, K. 2006. Physiological and energetic correlates of en route mortality for abnormally early migrating adult sockeye salmon (*Oncorhynchus nerka*) in the Thompson River, British Columbia. Can. J. Fish. Aquat. Sci. **63**: 1067–1077.

Zigler, S.J., Dewey, M.R., Knights, B.C., Runstrom, A.L., and Steingraeber, M.T. 2004. Hydrologic and hydraulic factors affecting passage of paddlefish through dams in the upper Mississippi River. Trans. Am. Fish. Soc. **133**(1): 160–172.

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Does size matter? A cautionary experiment on overoptimism in length-based bioresource assessment

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Abstract: Recently, there has been considerable progress in the development of neurolipofuscin-based age determination methods for crustacean stock assessment. Initial applications to lobster and crab fisheries suggest some important method-related differences between conventional length-based assessment parameter estimates and those derived with the new aging technique. Here, for the first time, we aim to clarify the basis for and implications of some of these discrepancies using an experimental fishery context. We estimate von Bertalanffy growth parameters (k and L_∞), longevity (t_{max}), total and natural mortality (Z and M, respectively), maximum sustainable relative yield-per-recruit (MSY′/R), and the exploitation rate that produces MSY′/R ($E_{MSY'/R}$) for a freshwater crayfish (*Pacifastacus leniusculus*) population by length–frequency analysis and tag–recapture (length-increment-at-length) and compare these results with simultaneous neurolipofuscin demographic estimates. Our central finding is that the length-based approaches are largely blind to the biological reality of asymptotic postmaturational growth, with the consequence that longevity is prone to underestimation, late growth trajectories and mortality rates to inflation, and sex differences to misjudgment. This inherent bias is likely to lead to pervasive undervaluing of potential yields and overly optimistic target exploitation rates that will heighten the risk of growth and recruitment overfishing. Neurolipofuscin offers a means of identifying and overcoming this important problem.

Résumé : Il y a eu beaucoup de progrès récemment dans le développement des méthodes de détermination de l'âge basées sur la neurolipofuscine pour l'évaluation des stocks de crustacés. Les premières utilisations dans les pêches de homards et de crabes ont révélé des différences importantes dues à la méthodologie entre la détermination conventionnelle des estimations des paramètres en fonction de la longueur et celle faite par les nouvelles méthodes d'estimation de l'âge. Nous cherchons ici, pour la première fois, à mettre en lumière la source de ces écarts et à en déterminer les conséquences dans le contexte d'une pêche expérimentale. Nous estimons les paramètres de croissance de von Bertalanffy k, L_∞, la longévité t_{max}, Z, les mortalités totale et naturelle, respectivement Z et M, le rendement relatif soutenable maximal par recrue MSY′/R et le taux d'exploiation qui permet $E_{MSY'/R}$ chez une population d'écrevisses d'eau douce (*Pacifastacus leniusculus*) par analyse de longueur–fréquence et par marquage–recapture (longueur-accroissement en fonction de la longueur) et comparons ces valeurs avec les estimations démographiques obtenues simultanément par la méthode à la neurolipofuscine. Notre découverte principale est que les méthodes basées sur la longueur ne tiennent en général pas compte de la réalité biologique de la croissance asymptotique après la maturation, ce qui a pour conséquence que la longévité a tendance à être sous-estimée, les trajectoires tardives de croissance et les taux de mortalité à être surestimés et les différences sexuelles à être mal évaluées. Ces erreurs inhérentes peuvent vraisemblablement mener à une sous-estimation généralisée des rendements potentiels et à des taux ciblés d'exploitation excessivement optimistes, ce qui augmente le risque de surpêche de la croissance et du recrutement. La méthode à la neurolipofuscine fournit un moyen d'identifier et de résoudre cet important problème.

[Traduit par la Rédaction]

Introduction

In an era of globally declining fisheries (Worm et al. 2006), the need for traditional- and ecosystem-based assessments to be underpinned by reliable population parameter estimates for target species is stark; inaccuracies can have devastating consequences (Myers et al. 1997; Campana 2001). Age-structured data are the preferred basis for modelling (Campana and Thorrold 2001), but this option has not been available for a major component of world annual cap-

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ture fishery production, i.e., the ~6 million tonnes valued at ~US$20 billion derived from crustaceans (FAO 2004), which are generally impossible to age by skeletal annuli. Consequently, stop-gap length-based methods involving the use of body size as a proxy for age have become the norm in crustacean stock assessment. However, the limitations of this approach are exemplified by a recent analysis of known-age microtag recaptures of restocked European lobster *Homarus gammarus* up to 10 years of age. This suggests that <5% of landings length variance is explained by age (Sheehy and Bannister 2002). In the last few years, there has been considerable progress in the development of a much-needed alternative in the form of neurolipofuscin-based crustacean age determination. Here, we provide an experimental case study of the way in which this novel technology can be used to identify and overcome important inherent weaknesses in length-based stock assessment.

Lipofuscin is a heterogeneous, lipoproteinaceous aggregate that accumulates predictably in normally aging eukaryotic cells as a result of imperfect catabolism (Terman and Brunk 2004). In arthropod neurons, this accumulation is strongly age-dependent, and several studies have shown that superior detection of annual cohorts can be achieved using neurolipofuscin concentration–frequency distributions (NCFDs) as opposed to length–frequency distributions (LFDs) (e.g., Sheehy et al. 1998; Bluhm et al. 2001; Kodama et al. 2006). Several experimental modulators of neurolipofuscinogenesis are known (e.g., Castro et al. 2002), but recent key findings for microtagged *H. gammarus* indicate that under complex and changeable natural environmental conditions, at least 93% of individual variation in neurolipofuscin concentration is explained by only two variables: chronological age and environmental temperature (Sheehy and Bannister 2002).

Neurolipofuscin-based aging is now beginning to inform stock assessments for commercially important species. Studies on *H. gammarus* (Sheehy et al. 1999; Sheehy and Shelton 2001; Sheehy and Bannister 2002) and the edible crab *Cancer pagurus* (Sheehy and Prior 2003, 2005*a*, 2007) have produced both similarities and important differences with earlier length-based parameter estimates. Our main purpose here is to help clarify, for the first time, the basis for some of the discrepancies and to consider their general implications for the validity of length-based assessment and resultant bioresource sustainability. To this aim, we use an experimental fishery context in the form of a pond population of freshwater crayfish, *Pacifastacus leniusculus*, to conduct a detailed comparison of assessment parameters estimated by traditional approaches, including length–frequency analysis and anniversary tag–recapture, with those simultaneously derived from neurolipofuscin demographics.

Materials and methods

Experimental fishery

Our experimental population of *P. leniusculus* was located in a pond at Ullesthorpe, Leicestershire, England (52°28.9′N, 1°14.6′W). This pond was isolated from other waterways and had a surface area of approximately 500 m^2. Mean annual water temperature was 10.3 °C (range 3.8–16.4 °C). We fished this population in July–August 1999 using baited cylindrical Swedish style traps with 40 mm mesh and sexed and measured the rostral carapace length (CL, mm) of all captures, of which there were 164 females and 132 males.

Length-based approaches

Length–frequency analysis

For each sex, we constructed an LFD with 2 mm class intervals (Guan and Wiles 1996). We analyzed the modal compositions of each LFD using PeakFit v. 4 (SPSS Inc., Chicago, Illinois). To minimize noise associated with the relatively small sample sizes that we obtained, we applied an automated fast Fourier transform (FFT) filtering routine to the frequency domain of each LFD. We selected a 6% smoothing window, since this gave the best overall noise reduction, while maintaining cohort resolution by comparison with previous results (Guan and Wiles 1996). Filtering involved removal of any linear trend, then a forward FFT, followed by zeroing of higher frequency components, an inverse FFT, and finally, restoration of any linear trend. Gaussian peaks of variable width were then fitted to the smoothed distribution by an automated least-squares fitting procedure. Peaks were first fitted to local maxima, then, based on analysis of the resulting residuals, any additional normal components were fitted. We disregarded any peaks with relative amplitudes ≤0.1 because we could not confidently discriminate these from noise. Peak resolution was assessed with the separation index (Sparre and Venema 1998), and length cohort ages were assigned by comparison with Guan and Wiles (1996), taking into consideration the low catchability of young-of-year and the 3 months delay between the main hatching period in May and our median sampling date.

Anniversary tag–recapture

Length increment-at-length data were obtained by anniversary tag–recapture. A total of 279 of the captured crayfish (150 females, mean CL = 51.9 mm, range 27–73 mm; and 129 males, mean CL = 50.1 mm, range 27–76 mm) survived anaesthetization in 0.25% clove oil and tagging by insertion of a 2 mm long numbered segment of spaghetti tag into the abdominal musculature and were returned to the pond. Intensive trapping to recapture tagged crayfish was conducted 1 year later (July–August 2000).

Age-based approach

Neurolipofuscin quantification and age determination

We measured neurolipofuscin concentration in the eyestalks of a random sample of 104 females and 81 males from the catch using histological and confocal image analysis methods similar to those described in Sheehy et al. (1996), Sheehy (2002), and the references cited therein. To determine the natural neurolipofuscin accumulation rate in the crayfish population, and so derive an age prediction model, we conducted a modal analysis on the NCFD from the above sample. To minimize effort while maximizing sample size (France et al. 1991), we pooled the male and female neurolipofuscin data (Sheehy et al. 1998). The justification for this was that unlike growth rate, no statistically significant ($p > 0.05$) sex differences have been found in neurolipofuscin accumulation patterns in *P. leniusculus* (Belchier et al. 1998) or any other arthropod species so far examined (Fonseca et

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al. 2005). For comparative purposes, the NCFD was otherwise configured in precisely the same way as the LFDs above, with the bulk of observations in the same number of bins, with identical smoothing, and again disregarding any peaks with relative amplitudes ≤0.1. By assuming an onset of neurolipofuscin accumulation in the first year of life in *P. leniusculus* (Belchier et al. 1998) and by fitting a linear regression to the progression of cohorts in the NCFD (Sheehy et al. 1998), we produced a neurolipofuscin-based age prediction model for *P. leniusculus* at the field site. We used this model to produce individual age estimates for each of the sampled crayfish, from which we then produced male and female age–length data and age–frequency distributions.

Assessment parameter estimation

We used standard, iterative, nonlinear regression procedures (SigmaPlot v. 4, SPSS Inc., Chicago, Illinois) to fit the von Bertalanffy model, with t_0 set to 0, to the neurolipofuscin-estimated age–length (NAL) data and to mean length-at-age observations obtained from LFD modal analysis. For the tag–recapture data, we fitted the Fabens (1965) construct of the von Bertalanffy model, which relates length increment to length at tagging and time at liberty. As is standard practice, we omitted zero growth observations, of which there was one female case.

We estimated mean maximum longevity, t_{max}, either arbitrarily as the average of the oldest 10% (e.g., Gust et al. 2002) of individual neurolipofuscin age estimates or as the estimated age of the oldest apparent LFD cohort.

Total mortality rate, Z, was estimated either directly from a neurolipofuscin-derived age distribution (age-structured catch curve) or by conversion of a length distribution to an age distribution (length-converted catch curve) using one of the von Bertalanffy growth curves obtained above. Length conversion and data point selection were undertaken with FiSAT II, v. 1.2.2 software (FAO, Rome). Z was estimated as the slope (with sign changed) of the linear regression fitting the descending right arm of each catch curve after application of a natural log to numbers in each age class and excluding partially recruited (ascending limb) and near-asymptotic (descending limb) age groups while maximizing sample size, according to the recommendations of Pauly (1990).

Natural mortality rate, M, was estimated by applying our age- and length-based t_{max} estimates to Hoenig's (1983) empirical model for unexploited stocks. For the purpose of generating standard errors and so as to be consistent with our t_{max} estimation method, we obtained multiple estimates of M by inserting the predicted ages of each of the oldest 10% of individuals into the model.

We then conducted a comparative assessment of relative yield-per-recruit, Y'/R (Beverton and Holt 1966), with FiSAT II under a range of hypothetical exploitation ratios, E. The various age- and length-based estimates of k, L_∞ and M obtained above were used in these assessments. We also employed our Z estimates in the yield model on the basis that $Z = M$ in our unexploited crayfish population. CL at first capture, L_c, was deemed to be 40 mm.

As a simple approximation, we tested for difference between each parameter (θ) estimated by the age-based method and the comparable estimates obtained by the length-based methods, using the estimates' standard errors (SEs) as obtained from multiple observations or iterative regression fitting. We employed either two-tailed t test or, where more than two treatments were compared, analysis of variance (ANOVA) with Bonferroni post hoc multiple comparison and the age-based estimate as a control. Significance testing of data in statistical summary format (θ, SE, n) was undertaken with SigmaStat v. 3.5 (Systat Software, Inc., Point Richmond, California).

Results

Cohort detection in length– and neurolipofuscin concentration – frequency distributions

Five putative cohorts, aged 2+ to 6+, were resolved in our female LFD (Fig. 1*a*), and four cohorts, aged 2+ to 5+, were resolved in our male LFD (Fig. 1*b*). However, at least eight putative female cohorts, ages 1+ to 8+, and five male cohorts, ages 1+ to 5+ were resolved in the NCFD (Fig. 1*c*), suggesting that the male and female 1+ cohort and the female 7+ and 8+ cohorts were sampled but not resolved in the respective LFDs. All separation indices were above a critical value of 2, i.e., at face value, all apparent modes were separable by standard modal analysis methods. The mean separation index of modes, which gave an overall indication of the resolution of apparent modes in the histograms, was 4.1 (range 2.8–7.4) in the NCFD. By comparison, it was 3.3 (range 3.0–3.8) in the female LFD and 4.0 (range 3.7–4.4) in the male LFD. If, however, the LFDs were assumed to contain the hidden cohorts indicated by the NCFD (1+, 7+, and 8+ female cohorts and 1+ male cohort) and these hidden cohorts were attributed separation indices of zero, then the mean separation indices for female and male LFDs fell to 1.9 and 3.0, respectively.

The progression of mean neurolipofuscin, NC, with age, T, was well defined by a linear model ($r^2 = 0.99$, $n = 8$, $p < 0.0001$):

$$(1) \qquad NC = 0.23T - 0.134$$

The progression of mean size-at-age in the female and male LFDs was well described by the von Bertalanffy model ($r^2 = 1.0$, $n = 5$, $p < 0.0001$ and $r^2 = 0.99$, $n = 4$, $p = 0.0002$, respectively).

Tag–recapture

After approximately 1 year, 33 tagged females (42–70 mm CL) and four tagged males (51–62 mm CL) were recaptured at the field site, representing recapture rates of 22% and 3%, respectively. Both male and female annual growth rates where inversely correlated with CL at release. A significant Fabens regression was achieved for females ($r^2 = 0.47$, $n = 32$, $p < 0.0001$), but the fit was marginally insignificant for males ($r^2 = 0.86$, $n = 4$, $p = 0.07$) (Table 1).

Neurolipofuscin-estimated age–length relationship

Both female and male NAL data were well fitted by von Bertalanffy models ($r^2 = 0.93$, $n = 104$, $p < 0.0001$ and $r^2 = 0.84$, $n = 81$, $p < 0.0001$, respectively) (Figs. 2*a* and 2*b*, respectively; Table 1). In Figs. 2*a* and 2*b*, the proximity to the growth curve of the intersects of drop-lines marking the three largest modes in the LFDs (Figs. 1*a* and 1*b*) and the

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Fig. 1. Modal analysis of frequency distributions of (*a*) female carapace length, (*b*) male carapace length, and (*c*) neurolipofuscin concentration (sexes combined) for the field population of *Pacifastacus leniusculus*: thin solid lines, best-fitting Gaussian components (very low amplitude peaks indistinguishable from noise were excluded); thick solid line, cumulative Gaussian fit; 1+ to 8+, annual cohort age designations.

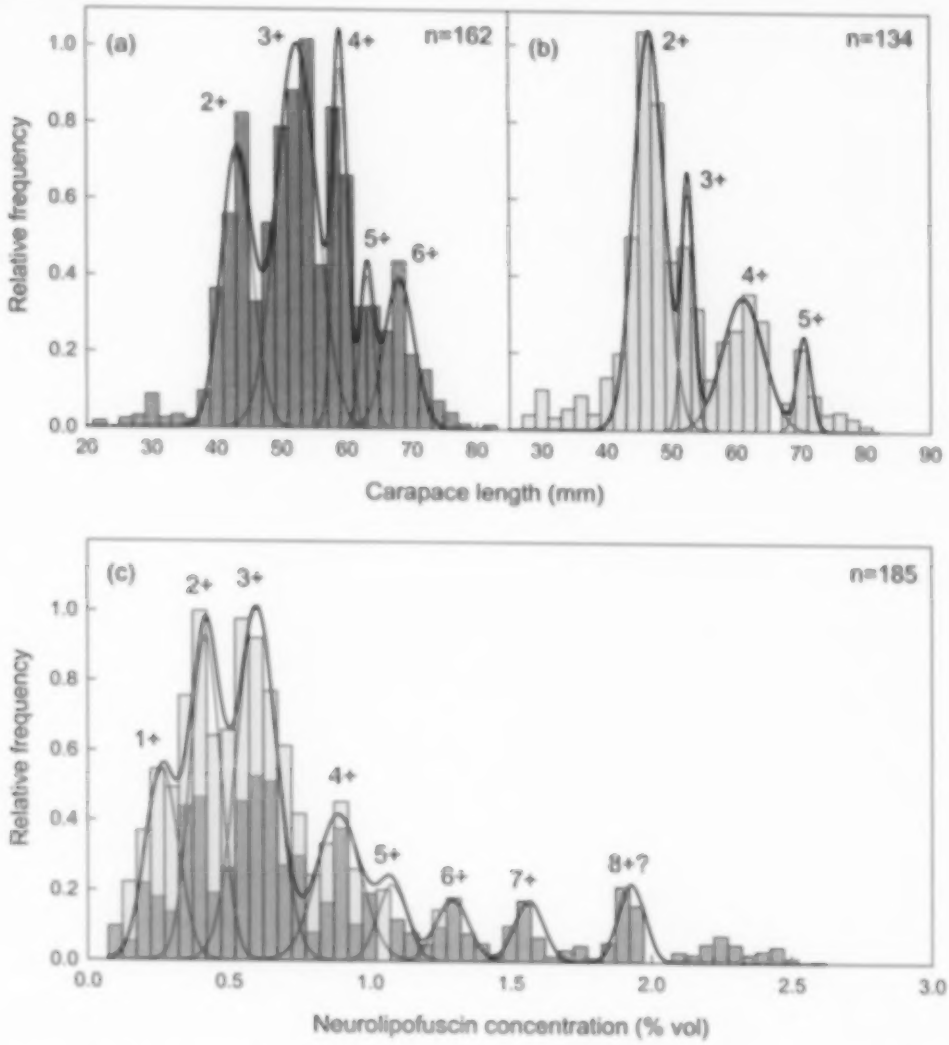

Table 1. von Bertalanffy growth parameters l_∞ and k (±SE) derived by length-based and neurolipofuscin age-based methods for the field population of *Pacifastacus leniusculus*, with a Bonferroni multiple comparison of differences using the age-based estimate as a control.

Method	Female			Male		
	l_∞	k	n	l_∞	k	n
Length-based: length–frequency	73.2±1.3NS	0.37±0.02NS	5	81.9±8.3*	0.33±0.07NS	4
Length-based: anniversary tag–recapture	74.9±4.3*	0.30±0.06*	32	76.1±7.1*	0.59±0.22NS	4
Age-based: neurolipofuscin age–length	64.5±0.39	0.50±0.01	104	64.3±0.92	0.55±0.02	81

Note: The respective length–frequency and tag–recapture estimates did not differ significantly from each other. *, significantly different to the control at $p < 0.05$; NS, not significantly different to the control.

NCFD (Fig. 1*c*) indicated that these peaks were derived principally from the same individuals, i.e., that the configuration of the major cohorts was conserved between the LFDs and the NCFD. However the female age–length data and NCFD showed several older age groups, close to asymptotic length, that were indistinguishable in the female LFD (Fig. 1*a*). On the other hand, the relatively right-truncated male NCFD (Fig. 1*c*) and NAL data (Fig. 2*b*) suggested that

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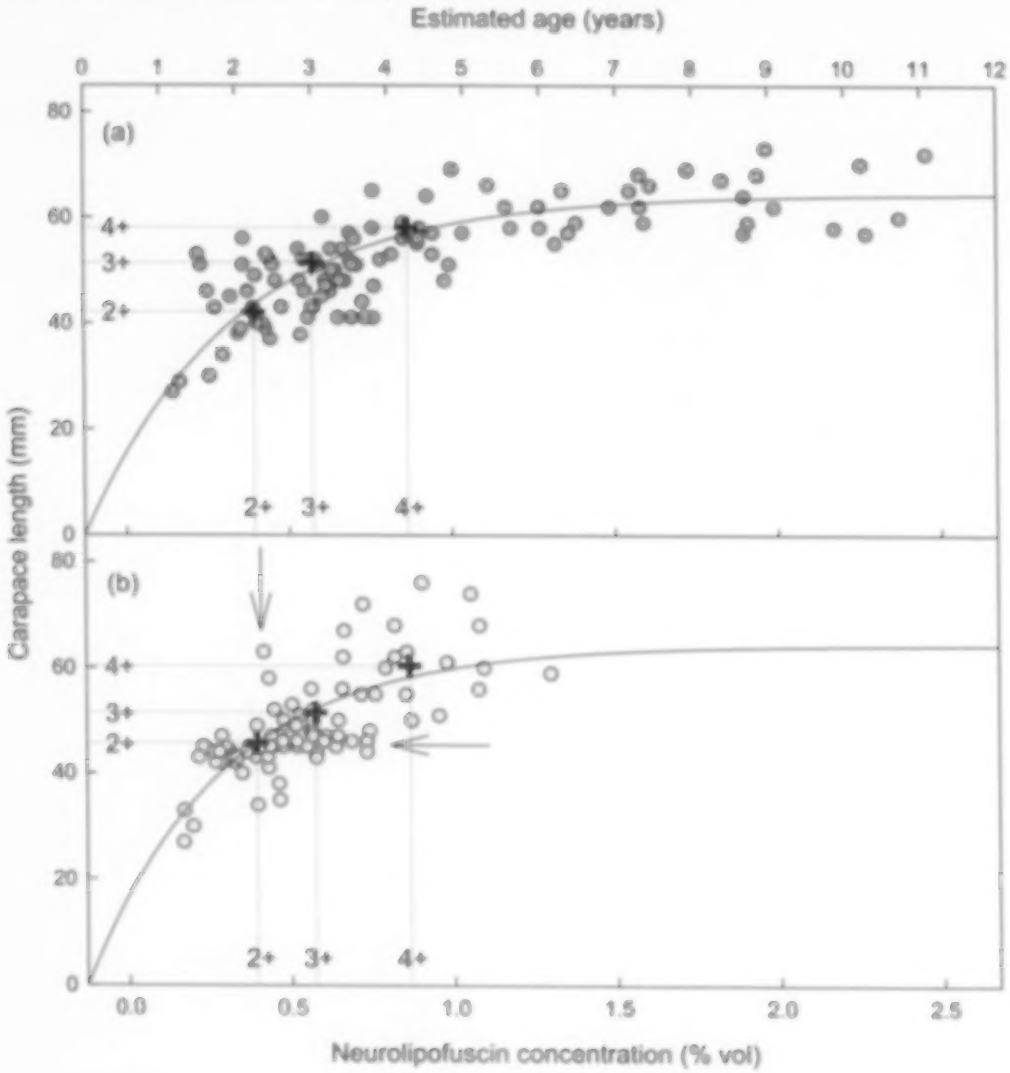
Fig. 2. Neurolipofuscin-estimated age–length relationships for the field population of *Pacifastacus leniusculus*: (*a*) females; (*b*) males; crosses and dotted drop lines, modal lengths vs. modal neurolipofuscin concentrations for the main cohorts 2+ to 4+ from Fig. 1; solid trend lines, best-fitting von Bertalanffy growth curves; horizontal and vertical arrows, evidence of size- and age-clustering of observations suggestive of instars and year classes, respectively.



the male LFD (Fig. 1*b*) was a reasonably good demographic representation. Horizontal and vertical clusters in the size-at-age data, particularly for males (Fig. 2*b*), were suggestive of instars and annual cohorts, respectively.

Length-converted and neurolipofuscin age-structured catch curves

The descending limbs of length-converted catch curves (e.g., Figs. 3*a* and 3*b*) showed far-right slope reductions that were not present in the comparable age-structured catch curves (Figs. 3*c* and 3*d*). This indicated that these slope reductions were due to proximity to the growth curve asymptote rather than to age-related shifts in mortality rate, and it necessitated exclusion of these data points from linear regression fits to determine *Z*. All regressions exhibited relatively low unexplained variance (r^2 = 0.73–0.98).

Comparison of parameter estimates

Generalized growth

There were no significant differences in L_∞ and k estimates derived from the two length-based methods (p = 0.30–0.88). However, the neurolipofuscin method produced estimates for both males and females that were, in several cases, significantly different from those generated from the length-based methods ($p < 0.001$) (Table 1). Note that despite their similarity to the female tag–recapture-based estimates, the female

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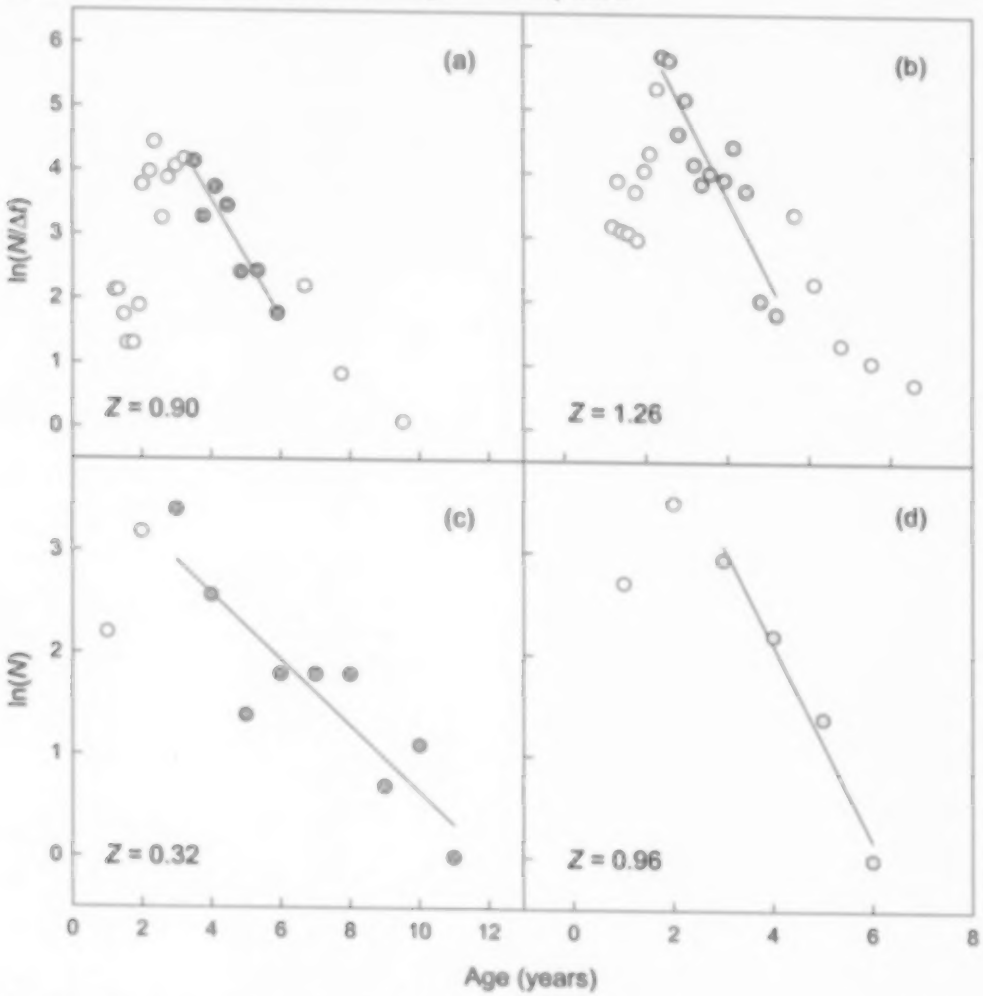
Fig. 3. Representative linearized catch curves for the field population of *Pacifastacus leniusculus*. (*a*, *c*) females, (*b*, *d*) males; (*a*, *b*) length-converted catch curves employing the length–frequency distribution-based growth curve for conversion; (*c*, *d*) neurolipofuscin-estimated age-structured catch curves; *N*, number of individuals in each age group or length slice; Δt, small time interval; shaded symbols, data used in analysis; open symbols, data excluded from analysis because of incomplete recruitment (ascending arm) or proximity to asymptote (descending arm); solid trend lines, best-fitting linear regressions defining total mortality rate, *Z*.



LFD-based L_∞ and k values were not significantly different from the age-based estimates according to Bonferroni ($p = 0.23$ and $p = 0.25$, respectively). However, they were significantly different by *t* test ($p < 0.001$ and $p = 0.006$, respectively). This discrepancy results from the conservative nature of the Bonferroni multiple comparison and the low sample size in the LFD-based analysis. Age-based estimates of L_∞ were lower and k generally higher than the length-based estimates. For all methods, the L_∞ estimates for males represented extrapolations because of the lack of old males in the population.

Total mortality rate

All length-based estimates of *Z* were significantly different from the age-based estimates ($p < 0.001$), with the exception of the LFD estimate for males ($p = 0.109$). Female and male length-based *Z* estimates where 91%–181% and 31%–92% higher than the age-based estimates, respectively (Table 2). Length-based estimation sometimes substantially underestimated sex difference in *Z*.

Longevity

The age-based estimate of t_{max} for females (9.7 years) was significantly different from ($p = 0.0058$) and 54% higher than the age of the oldest apparent length cohort (6.3 years) (Table 2). There was no significant difference ($p = 0.72$) between the age- (5.1 years) and length-based (5.3 years) t_{max} estimates for males. The length-based approach substantially underestimated the sex difference in longevity.

Natural mortality rate

As *M* derived directly from t_{max}, method-related patterns in the former closely mirrored those in the latter. The length-

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Table 2. Parameter values (±SE) derived by length-based and neurolipofuscin age-based methods for the field population of *Pacifastacus leniusculus*, with two-tailed *t* test or Bonferroni multiple comparison of differences using the age-based estimate as a control.

Parameter	Method	Female	Male	% sex difference
t_{max} (years)	Length-based: oldest apparent length–cohort age	6.3* (1)	5.3NS (1)	19
	Age-based: oldest 10% of neurolipofuscin age estimates (control)	9.7±0.28 (10)	5.1±0.18 (8)	90
M (year^{-1})	Length-based: Hoenig model using length-based t_{max}	0.69* (1)	0.82NS (1)	19
	Age-based: Hoenig model using age-based t_{max} (control)	0.46±0.01 (10)	0.86±0.02 (8)	87
Z (year^{-1})	Length-based: catch curve converted using length–frequency-based growth curve	0.90±0.06* (7)	1.26±0.05NS (12)	40
	Length-based: catch curve converted using tag–recapture-based growth curve	0.61±0.01* (11)	1.84±0.07* (12)	202
	Length-based: catch curve converted using neurolipofuscin age–length-based growth curve	0.88±0.09* (5)	1.84±0.14* (6)	109
	Length-based: catch curve converted using neurolipofuscin age distribution (control)	0.32±0.05 (9)	0.96±0.11 (4)	200
	Age-based: catch curve using neurolipofuscin age distribution (control)			

Notes: t_{max}, longevity; M, natural mortality; Z, total mortality; numbers in parentheses are sample sizes. *, significantly different to the control at $p < 0.05$; NS, not significantly different to the control.

based estimate of M for females (0.69) was significantly different from ($p = 0.0004$) and 50% higher than the corresponding age-based estimate (0.46) (Table 2). There was no significant difference ($p = 0.61$) between the length- (0.82) and age-based (0.86) estimates of M for males. The length-based approach substantially underestimated the sex difference in M.

Maximum sustainable relative yield-per-recruit and exploitation rate

The age-based estimates of MSY′/R (Table 3) were 175%–700% and 100%–400% higher than the corresponding length-based estimates for males and females, respectively. For females, the optimum $E_{MSY'/R}$ values predicted by the length-based approaches were 9%–35% higher than those predicted from age. No clear method-related difference in $E_{MSY'/R}$ was found for males. Length-based approaches underestimated sex difference in $E_{MSY'/R}$.

Discussion

The basis for neurolipofuscin demographic analysis in fisheries research

At the cellular level, neurolipofuscin is an aging biomarker that appears to be fundamentally and universally involved in the process of biological senescence (Fonseca et al. 2005). At the population level, seasonal reproduction generates temporally clustered demographic groups (cohorts) that are manifested analogously as modes in both LFDs and NCFDs. While modal progression in an LFD indicates generalized growth trajectory, in an NCFD it indicates neurolipofuscin accumulation rate. The latter has been confirmed by analysis of seasonal changes in neurolipofuscin accumulation rate in time series of NCFDs (Kodama et al. 2006) and by control studies on known-age individuals (Sheehy et al. 1998). The present study provides further evidence of this in that our NCFD-estimated neurolipofuscin accumulation rate (0.234% vol·year^{-1}) for *P. leniusculus* was almost identical to that previously reported (0.237% vol·year^{-1}) for known-age individuals of this species reared in the laboratory at ambient temperatures (Belchier et al. 1998). Modes in NCFDs do not correspond to instars (cf. Phillips et al. 1983; Sheehy et al. 1998), and neurolipofuscin accumulation rate is decoupled from both moult frequency (cf. Guan and Wiles 1996; Belchier et al. 1998) and growth rate (e.g., Sheehy 1990; O'Donovan and Tully 1996; Wahle et al. 1996). We speculate that this decoupling may reflect the underlying ability of the brain to differentially activate anabolic and catabolic pathways (Szekely and Szelenyi 2005).

Although we cannot exclude the possibility that an additional cohort exists in the NCFD between our 7+ and 8+ designations, we otherwise found strong indications from the varying separation indices that the annual average neurolipofuscin rate in *P. leniusculus* differs between years, as would be expected from average annual temperature variations (Sheehy and Bannister 2002). However, simulations have shown that marked interannual variations will still give rise to a highly linear neurolipofuscin accumulation pattern (Sheehy and Bannister 2002).

The prediction that cohorts in NCFDs would be better resolved than those in LFDs for the same sample (Sheehy et

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Table 3. Comparison of Beverton–Holt relative yield-per-recruit (*Y*/*R*) assessments for the field population of *Pacifastacus leniusculus*, as estimated by length-based and neurolipofuscin age-based methods.

		Female		Male			
Method	Sources of M, k, and L_∞	MSY/R	$E_{MSY/R}$	MSY/R	$E_{MSY/R}$	% sex difference in $E_{MSY/R}$
Length-based	Hoenig model with length-based t_{max}, length–frequency-based growth curve	0.04	0.85	0.02	0.86	1
	Catch curve converted with length–frequency-based growth curve	0.02	1.00	0.01	1.00	0
	Catch curve converted with tag–recapture-based growth curve	0.03	0.86	0.01	1.00	16
	Catch curve converted with neurolipofuscin age–length-based growth curve	0.04	1.00	0.01	1.00	0
Age-based	Hoenig model with age-based t_{max}, neurolipofuscin age–length-based growth curve	0.11	0.78	0.05	0.93	20
	Catch curve using neurolipofuscin age distribution, age–length-based growth curve	0.16	0.74	0.04	1.00	35

Note: M, natural mortality rate (= total mortality rate, Z, in this unexploited population); k and L_∞, von Bertalanffy growth parameters; MSY/R, maximum sustainable relative yield-per-recruit; $E_{MSY/R}$, exploitation ratio producing MSY/R.

al. 1994) has now been borne out for several species (Table 4), including *P. leniusculus* in the present study. The basis for this appears to be threefold. First, as suggested by the present results, the selection ogive of the capture gear may directly crop the LFD, potentially obscuring peaks such as the 1+ cohort in trap-caught *P. leniusculus* samples, but this only has an indirect effect on the shape of the NCFD. Second, growth rate typically declines more with age than neurolipofuscin accumulation rate (Sheehy 1992). Consequently, as exemplified by the present results, the overlap of cohorts at asymptotic length in LFDs is not a problem in NCFDs. Third, age-specific variation in neurolipofuscin concentration is usually less variable than size-at-age (e.g., Sheehy 1990; Belchier et al. 1998; Sheehy and Bannister 2002), producing NCFD normal components with lower standard deviations and thus higher separation indices (Sheehy et al. 1994). Cross-sectional studies on a range of crustacean species suggest that individual variability explains <10% of the variance in neurolipofuscin concentration over the lifespan of a cohort, with chronological age and environmental temperature explaining >90% (e.g., Sheehy 1990; Belchier et al. 1998; Sheehy and Bannister 2002).

A note of clarification will be helpful here. Some studies on known-age crustaceans appear to have shown that age-specific individual variation in neurolipofuscin concentration is similar to or greater than variation in size, but in each case this result seems to arise from error or artifact. In Sheehy (1992, fig. 1), pond-reared freshwater crayfish, *Cherax quadricarinatus*, reportedly showed r^2 values of 95.3%, 95.9%, and 78% for age vs. neurolipofuscin concentration, CL, and body mass, respectively. The latter two values are typographical errors and should be 75.9% and 62%, respectively. For pond-reared *Penaeus japonicus*, the r^2 value for age vs. body mass reported by Vila et al. (2000) was artificially reduced by the selective removal of all large, market-size prawns at 11.2 month of age, which the authors noted in their methods. This size selection would have had little effect on observed neurolipofuscin variability. For a subsample of Norwegian restocked *H. gammarus*, Uglem et al. (2005) reported an r^2 value for age vs. CL of 0.78, which is unusually high for microtag recaptures of this species. However, the authors implied that their subsample was biased by a truncated 2-year tag–recapture period that precluded recapture of slow growers. Elsewhere in the paper, they reported that "for a linearly transformed dataset consisting of all recaptured males and females (n = 877, ages: 3–13 years)", the r^2 was only 11.2%. The latter figure is more in line with expectations from other microtag studies (r^2 = 2%, Sheehy et al. 1996; r^2 = 0%, Sheehy et al. 1999). For laboratory-reared juvenile *H. gammarus* and *Homarus americanus*, O'Donovan and Tully (1996) and Wahle et al. (1996) reported high r^2 values for age vs. CL of 90.3% and 92.2%, respectively. However, the authors considered growth variability to have been artificially reduced by the unnatural availability of equivalent living spaces and the absence of social interactions. Reduced growth variability in the laboratory compared with the field has also been noted for the Western Australian rock lobster, *Panulirus cygnus* (Chittleborough 1976). As a whole, these findings highlight the pitfalls associated with use of captive growth as a proxy for that in the wild. By contrast, age-specific individual variability in neurolipofuscin concen-

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Table 4. Comparison of numbers of cohorts detected in length- and neurolipofuscin concentration-frequency distributions for various natural crustacean populations.

	Female			Male		
Species (reference)	Length	Neurolipofuscin	% difference	Length	Neurolipofuscin	% difference
Panulirus cygnus (Sheehy et al. 1998)	4 (1+ to 4+)	6 (1+ to 6+)	50	4 (1+ to 4+)	5 (1+ to 5+)	25
Notocrangon antarcticus (Bluhm and Brey 2001)	2 (?)	8 (3+ to 10+)	300	1 (?)	4 (3+ to 6+)	300
Waldeckia obesa (Bluhm et al. 2001)	2 (?)	5 (1+ to 5+)	150	2 (?)	5 (1+ to 5+)	150
Cancer pagurus (Sheehy and Prior 2006*b*, 2007)	5 (3+ to 7+)	8 (2+ to 9+)	29	4 (4+ to 7+)	5 (4+ to 8+)	15
Orutanoguilla eruberis (Kodama et al. 2005)	2 (1+ to 2+)	4 (1+ to 4+)	100	2 (1+ to 2+)	4 (1+ to 4+)	100
Pandalus latirostris (this study)	5 (2+ to 6+)	8 (1+ to 8+)	33	4 (2+ to 5+)	5 (1+ to 5+)	0
Average			110			98

Note: Numbers in parentheses are reported cohort age ranges in years; ?, specific ages not assigned; % difference refers to the differences in the ages of the oldest apparent cohorts or, where no specific cohort ages are reported, to the differences in the number of cohorts resolved by length and neurolipofuscin concentration.

tration, as well as being lower than that for size, appears to be highly conserved across species and environments (Sheehy and Bannister 2002).

Even the best length–frequency distribution can be highly misleading

Often, LFDs are of very limited value for age determination because cohorts are not distinguishable. On first inspection, the same cannot be said for our length compositions for *P. leniusculus*. These are among the best likely to be encountered for any crustacean and would normally instill confidence in the demographic estimates derived from them. However, our comparison with the NCFD shows that even the best LFD can be misleading. Neurolipofuscin analysis indicates the presence of many hidden age classes in the female LFD but not in the male LFD. The conclusion is that even an LFD with well-formed modes and all separation indices above the critical value of 2 is not necessarily a reliable representation of population age structure. Can these findings be generalized? Results from neurolipofuscin studies on other crustaceans (Table 4) strongly suggest that they can; for both sexes, LFDs consistently under-represent, by half on average, the number and (or) maximum age of cohorts in samples by comparison with NCFDs for the same samples. Just as for finfish aging by otoliths (Campana 2001), we have found in the present case that it is the older individuals that are most difficult to age accurately by conventional methods, although they are most influential for estimation of growth, mortality, and longevity. As the present case demonstrates, such errors can have extremely important downstream implications for stock assessment and management.

Missed older cohorts in LFDs and mean length-at-age fits bias L_∞ upward

For females, the high LFD-based L_∞ by comparison with the NAL estimate is, in part, the result of obscuration of the older half of the age groups in the LFD, all approaching asymptotic length. However, this does not easily explain the high male L_∞ by LFD because, as we have noted, the latter was a reasonably good demographic representation. Instead, we assume that our adherence to the established practice of fitting the growth curve to mean length-at-age derived from modal analysis resulted in loss of relevant information on age-specific growth variability, resulting in biased parameter estimation (Rosenberg and Beddington 1987; Isaac 1990).

Common problems with tag–recapture: model construct discrepancies and low recovery

Tagging-related injury sometimes depresses growth rate, but we see no evidence of this in our results by comparison with the other methods. Given the relatively good return rate and size range of tag–recaptured females, differences in the growth parameters estimated by tagging and NAL for this sex appear to be due to basic differences in the von Bertalanffy model constructs used in each method, in particular the fact that L_∞ means asymptotic mean length-at-age for age–length data and maximum length for anniversary tagging data (Francis 1988; James 1991). In addition, the tag–recapture growth curve represents average growth in the recaptured size range for a particular relatively short period

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at liberty, whereas the NAL curve represents growth integrated over the whole life of each individual sampled.

For males, as well as parameter differences due to the two different model constructs employed, we achieved very low tag recovery ($n = 4$), not unlike the samples sizes that on occasion have had to be used in actual stock assessments (e.g., Addison and Bennett 1992). The size range of male recaptures (51–62 mm CL) was also extremely limited, being only a fifth of the full size range of males encountered during the study (27–76 mm CL). This situation closely parallels that for many trap fisheries in which gear selectivity, catchability biases, and high mortality rates result in relatively restricted landings size ranges that produce heavily biased growth trajectories (e.g., Sheehy et al. 1999). As a consequence, in the present study, tag–recapture-based male growth parameters were estimated with low precision.

Different length-based methods give similar results, but two wrongs do not make a right

The lack of a statistically significant difference between our growth parameter estimates obtained by the two length-based methods is noteworthy. Fisheries literature often correctly emphasizes the need for parameter estimates obtained by one method to be validated by another before acceptance. However, the present study highlights that mutually reinforcing results are not necessarily correct results. In the present case, tag–recapture and length–frequency appear to have produced equally erroneous outcomes despite their different underlying sources of bias.

Overestimation of *Z*: the length-based catch curve is blind to mature, slow-growing ages

The exponential decay of cohorts over time, as defined by the Z parameter, is a cornerstone of classical theory of exploited fish stocks (Sparre and Venema 1998), and Z is a base input for modern Ecopath–Ecosim ecosystem modeling (Christensen and Walters 2004). Z is typically also used to derive two other critical parameters: fishing mortality rate ($F = Z - M$) and exploitation rate ($E = F/Z$). It has been stated recently that the estimation of mortality parameters for decapod crustaceans through the use of age-based models is impossible, because age determination is difficult and time-consuming (Woll et al. 2006). In fact, crustacean mortality estimates were readily produced with the neurolipofuscin technique in this study and previous ones (Sheehy et al. 1998; Bluhm and Brey 2001; Bluhm et al. 2001), demonstrating that the above statement is not informed.

The consistent overestimation of Z by length-based methods that we observed appears to be due, in part, to bias in the underlying length-based growth curves. Because these overestimated the asymptote and underestimated the curvature, they biased the conversion of length classes toward younger ages. However, the female NAL-based growth curve, which was not subject to problems associated with missing data at the upper end of the age range, still resulted in overestimation of Z when applied to length conversion. This highlights a more fundamental weakness in the length-converted catch curve approach — it cannot discriminate older age classes lying at or near asymptotic length, as occurred for females in the present study. Indeed, because of the general assumption that underlies length-based approaches that differences in size can be validly related to differences in age breaks down near the asymptote, it is standard practice for this portion of the length distribution to be excluded from the mortality computations (Pauly 1990; Sparre and Venema 1998). This practice conveniently sidesteps a modeling inadequacy, but it does not necessarily make the resultant Z any more reliable because it effectively eliminates the most important age classes for estimating mortality. In our age-structured catch curves, we found no evidence of a shift in Z in older age groups that could provide an alternative explanation for the apparent biases in the length-based estimates that omit these age groups. Likewise, we found no evidence that seasonalized growth was responsible for the bias (Pauly 1990; Sparre 1990). These discrepancies in length- and age-based Z estimates deserve a fuller mathematical investigation than is possible within the scope of the present paper.

Lipofuscin: key to the most important yet elusive assessment parameters, t_{max} and *M*

M continues to be one of the most important yet least well-estimated parameters in fishery models (Hewitt and Hoenig 2005). With very few exceptions, models of fish stock dynamics include M as a parameter and are often highly sensitive to the value of M used and its interaction with other model parameters (Vetter 1988). The difficulty in measuring this parameter directly has seen the development of alternative approaches, such as the prediction of M from its inverse relationship with longevity, t_{max} (Hoenig 1983). The latter approach has, in itself, proved problematic for many species because of the difficulty in estimating their lifespan, as exemplified by our attempts to determine the lifespan of female *P. leniusculus* by established length–frequency techniques. Neurolipofuscin analysis overcomes these problems. It is noteworthy that although there was only a 3.4-year difference in the length- and age-based t_{max} estimates for female *P. leniusculus*, an equivalent relative error (54%) for a very long-lived species such as *H. gammarus* (Sheehy and Bannister 2002) would equate to some 20 years. For male *P. leniusculus*, the relative similarity of t_{max} estimates from both methods is attributable to the paucity of age groups in the population at asymptotic length, where the length-based approach would otherwise malfunction.

Length-based approaches misjudge sex differences in population parameters and $E_{MSY/R}$

We found that that the consistent underestimation of sex differences in t_{max}, Z, and M by the length-based approaches was ultimately manifested in relative yield-per-recruit assessments that failed to correctly predict sex differences in $E_{MSY/R}$. The pervasive use of such approaches in fisheries may be contributing, therefore, to widespread failure to implement appropriate sex-specific management regimes.

Length-based parameter biases force MSY′/*R* down and increases overfishing risk

Our assessments consistently demonstrated substantial underestimation of MSY′/R by the length-based methods. This was a direct result of the relatively high M and L_∞ values and low k values employed in the length-based yield calculations, which, by comparison with the age-structured ap-

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proaches, underestimate natural survivorship and growth rate and thus the proportion of the gain in biomass from individual growth that would normally accrue in the population from year to year in the absence of fishing. It is generally the case that a higher estimate of M would generate a higher optimum exploitation rate to catch fish before they die of natural causes (Vetter 1988), and we observed this effect for females in the present study. All length-based $E_{MSY/R}$ estimates exceeded the optimal exploitation rates predicted by age-based methods. Overestimation of M in populations with low M may also hide the sensitivity of yield-per-recruit to exploitation rate and increase the risk of growth overfishing with severe reduction of total yield if $E_{MSY/R}$ is exceeded. An overly optimistic $E_{MSY/R}$ would also unnecessarily reduce relative biomass-per-recruit, heightening the risk of spawning stock depletion and recruitment overfishing (Sparre and Venema 1998). The widely used cohort analysis is particularly sensitive to error in M, which accumulates as the analysis proceeds backward in time (Vetter 1988).

Length compositions hide recruitment relationships

Accounting for the way in which the environment and adult population size affect juvenile survival and recruitment to the exploitable stock is an important component of stock assessment. Although a comparative analytical treatment of recruitment relationships was beyond the scope of the present study, we have shown elsewhere that variability in length-at-age can completely obscure, in a length composition, strong environmental signals that are otherwise clearly visible as year-class strength fluctuations in the companion neurolipofuscin-based age composition. Major changes in stock structure are known to occur without changes in landings length compositions (Sheehy and Bannister 2002), and the implication is that use of apparently stable length compositions to assess stock status may result in a static management regime being applied to situations where the setting of annually variable controls is more appropriate. In such circumstances, year-class failures may not be detected, and a management response may not be mounted until long after the event.

It has been shown elsewhere (Sheehy 2001; Zabel and Levin 2002) that uncertainty in the estimated age distribution of a fishery's recruiting length class produces profoundly misleading artefactual curvature in the perceived spawner–recruit relationship. This curvature has previously been taken to imply that density-dependent compensatory mortality of juveniles occurs above a certain fairly low adult stock size, i.e., that there is an oversupply of offspring, when in fact no such mechanism of resilience to exploitation may exist at the stock sizes in question. Misinterpretation of the curvature of perceived spawner–recruit relationships has almost certainly resulted in inadequate protection for the spawning stock and major losses in some fisheries (Zabel and Levin 2002).

Size does matter!

The value of the present study is that it is a rare example of an experimental comparison of the performance of well-established but distinctly different approaches to population analysis. On the basis of our findings, and in answer to our opening question, we conclude that size does matter in so far as the pervasive application of stop-gap stock assessment methods that employ size "as an indicator of biological population parameters" and that "require little investment" (Woll et al. 2006) may well be resulting in or enabling systematic overexploitation of valuable bioresources.

Our results focus attention on a quintessential weakness of size-based methods — the inability to resolve a succession of mature age groups in the catch under the prevailing biological reality of variable and asymptotic post-maturational growth. If length-based methods miss older cohorts, error propagation with major consequences for downstream assessment is not at all surprising. What is alarming, however, is how widespread the application of these techniques is for assessment of very valuable resources for want of better alternatives. The modern history of finfisheries is littered with examples in which age underestimation has resulted in overly optimistic assessments of growth and mortality rate, in turn contributing to serious overexploitation (Campana 2001).

Based on their data for microtagged *H. gammarus*, Uglem et al. (2005) speculated that under some circumstances, length may provide a sufficiently accurate estimate of age in a considerably more time- and cost-effective manner than quantification of lipofuscin. However, as noted above, this surprising proposal appears to be based on a selective and highly unusual subsample. It also begs the question as to exactly what circumstances relevant to stock assessment of *H. gammarus* the authors might be referring to. Length-based assessments often involve measurements of many tens of thousands of individuals (e.g., Woll et al. 2006), whereas we have shown here that with a modicum of expertise, neurolipofuscin can be used to produce superior age-base parameter estimates at a small fraction of the above sample size, in timely fashion, and at minimal expense. Economies of scale are also likely. We maintain that while size measurements can be useful for some purposes other than age determination, such as indices of fecundity or condition, knowing an individual's age is what really counts. Physiological age determines important life-history milestones such as maturation and longevity, and chronological age is ultimately the foundation of all robust demographic analyses, irrespective of the proxies employed. We invite fisheries scientists, particularly from developed countries, to make the investment in moving on from simplistic and outdated length-based assessment approaches that risk harm to valuable resources. Neurolipofuscin demographic techniques have made considerable progress in recent years, with successful applications not only to the Crustacea, but also to other groups where traditional approaches are inadequate (e.g., Lomovasky et al. 2002). In addition, as neurolipofuscin quantification methods become more streamlined, this remarkable pigment will have a wider role to play in helping us understand and ameliorate the impacts of the other pressing sources of ecosystem stress, namely climate change (e.g., Sheehy and Bannister 2002), invasive species (e.g., Belchier et al. 1998), and pollution (e.g., Byrne and O'Halloran 2000).

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References

Addison, J., and Bennett, D. 1992. Assessment of minimum landing sizes of the edible crab, *Cancer pagurus*, on the east coast of England. Fish. Res. **13**: 67–88. doi:10.1016/0165-7836(92)90034-Q.

Belchier, M., Edsman, L., Sheehy, M.R.J., and Shelton, P.M.J. 1998. Estimating age and growth of long-lived temperate freshwater crayfish using lipofuscin. Freshw. Biol. **39**(3): 439–446. doi:10.1046/j.1365-2427.1998.00292.x.

Beverton, R.J.H., and Holt, S.J. 1966. Manual of methods for fish stock assessment. Part 2. Tables of yield functions. United Nations Food and Agriculture Organization, Rome, Italy. UN FAO Fisheries Tech. Pap. No. 38 (Rev. 1).

Bluhm, B.A., and Brey, T. 2001. Age determination in the Antarctic shrimp *Notocrangon antarcticus* (Crustacea: Decapoda), using the autofluorescent pigment lipofuscin. Mar. Biol. **138**(2): 247–257. doi:10.1007/s002270000458.

Bluhm, B.A., Brey, T., and Klages, M. 2001. The autofluorescent age pigment lipofuscin: key to age, growth and productivity of the Antarctic amphipod *Waldeckia obesa* (Chevreux, 1905). J. Exp. Mar. Biol. Ecol. **258**(2): 215–235. doi:10.1016/S0022-0981(01)00214-3.

Byrne, P.A., and O'Halloran, J. 2000. Acute and sublethal toxicity of estuarine sediments to the Manila clam, *Tapes semidecussatus*. Environ. Toxicol. **15**(5): 456–468. doi:10.1002/1522-7278(2000)15:5<456::AID-TOX14>3.0.CO;2-9.

Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. **59**(2): 197–242. doi:10.1111/j.1095-8649.2001.tb00127.x.

Campana, S.E., and Thorrold, S.R. 2001. Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? Can. J. Fish. Aquat. Sci. **58**(1): 30–38. Available from pubs.nrc-cnrc.gc.ca/cgi-bin/rp/rp2_abst_e?cjfas_f00-177_58_ns_nf_cjfas1-01 [accessed 1 July 2006].

Castro, M., Encarnação, P., and Tully, O. 2002. The effect of dietary antioxidants on lipofuscin accumulation in the crustacean brain. J. Exp. Mar. Biol. Ecol. **269**(1): 53–64. doi:10.1016/S0022-0981(01)00388-4.

Chittleborough, R.G. 1976. Growth of juvenile *Panulirus longipes cygnus* George on coastal reefs compared with those reared under optimal environmental conditions. Aust. J. Mar. Freshw. Res. **27**(2): 279–295. doi:10.1071/MF9760279.

Christensen, V., and Walters, C.J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecol. Model. **172**(2–4): 109–139. doi:10.1016/j.ecolmodel.2003.09.003.

Fabens, A.J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth, **29**(3): 265–289.

FAO. 2004. Yearbooks of fishery statistics. Summary Tables 2004. Appendix II — World fishery production: estimated value by groups of species. United Nations Food and Agriculture Organization, Rome, Italy. Available from www.fao.org/fi/statist/statist.asp [accessed 17 July 2007].

Fonseca, D.B., Brancato, C.L., Prior, A.E., Shelton, P.M.J., and Sheehy, M.R.J. 2005. Death rates reflect accumulating brain damage in arthropods. Proc. R. Soc. Lond. B Biol. Sci. **272**(1575): 1941–1947. doi:10.1098/rspb.2005.3192.

France, R., Holmes, J., and Lynch, A. 1991. Use of size–frequency data to estimate the age composition of crayfish populations. Can. J. Fish. Aquat. Sci. **48**(12): 2324–2332.

Francis, R.I.C.C. 1988. Are growth parameters estimated from tagging and age–length data comparable? Can. J. Fish. Aquat. Sci. **45**(6): 936–942.

Guan, R., and Wiles, P.R. 1996. Growth, density and biomass of crayfish, *Pacifastacus leniusculus*, in a British lowland river. Aquat. Living Resour. **9**(3): 265–272.

Gust, N., Choat, J.H., and Ackerman, J.L. 2002. Demographic plasticity in tropical reef fishes. Mar. Biol. **140** (5): 1039–1051. doi:10.1007/s00227-001-0773-6.

Hewitt, D., and Hoenig, J.M. 2005. Comparison of two approaches for estimating natural mortality based on longevity. Fish. Bull. **103**(2): 433–437. Available from fishbull.noaa.gov/1032/hewitt.pdf [accessed 1 July 2006].

Hoenig, J.M. 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. **81**(4): 898–903. Available from www.fisheries.vims.edu/hoenig/pdfs/Hoenig_EmpiricalUseOfLongevityData.pdf [accessed 1 July 2006].

Isaac, V.J. 1990. The accuracy of some length-based methods for fish population studies. International Center for Living Aquatic Resources Management, Manila, the Philippines. ICLARM Tech. Rep. No. 27.

James, I.R. 1991. Estimation of von Bertalanffy growth curve parameters from recapture data. Biometrics, **47**: 1519–1530. Available from www.jstor.org/view/0006341x/di009382/00p0196i/0 [accessed 1 July 2006].

Kodama, K., Yamakawa, T., Shimizu, T., and Aoki, I. 2005. Age estimation of the wild population of Japanese mantis shrimp *Oratosquilla oratoria* (Crustacea: Stomatopoda) in Tokyo Bay, Japan, using lipofuscin as an age marker. Fish. Sci. **71**(1): 141–150. doi:10.1111/j.1444-2906.2005.00941.x.

Kodama, K., Shiraishi, H., Morita, M., and Horiguchi, T. 2006. Verification of lipofuscin-based crustacean ageing: seasonality of lipofuscin accumulation in the stomatopod *Oratosquilla oratoria* in relation to water temperature. Mar. Biol. **150**(1): 131–140. doi:10.1007/s00227-006-0337-x.

Lomovasky, B.J., Morriconi, E., Brey, T., and Calvo, J. 2002. Individual age and connective tissue lipofuscin in the hard clam *Eurhomalea exalbida*. J. Exp. Mar. Biol. Ecol. **276**(1–2): 83–94. doi:10.1016/S0022-0981(02)00240-X.

Myers, R.A., Hutchings, J.A., and Barrowman, N.J. 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. Ecol. Appl. **7**(1): 91–106. Available from www.jstor.org/view/10510761/di986046/98p0201q/0 [accessed 1 July 2006].

O'Donovan, V., and Tully, O. 1996. Lipofuscin (age pigment) as an index of crustacean age: correlation with age, temperature and body size in cultured juvenile *Homarus gammarus* L. J. Exp. Mar. Biol. Ecol. **207**(1–2): 1–14. doi:10.1016/S0022-0981(96)02662-7.

Pauly, D. 1990. Length-converted catch curves and the seasonal growth of fishes. Fishbyte, **8**: 33–38.

Phillips, B.F., Joll, L.M., Sandland, R.L., and Wright, D. 1983. Longevity, reproductive condition and growth of the western rock lobster, *Panulirus cygnus* George, reared in aquaria. Aust. J. Mar. Freshw. Res. **34**(3): 419–429. doi:10.1071/MF9830419.

Rosenberg, A.A., and Beddington, J.R. 1987. Monte-Carlo testing of two methods for estimating growth from length–frequency data with general conditions for their applicability. *In* Length-based methods in fisheries research. ICLARM Conference Proceedings, Vol. 13. Proceedings of the International Conference on the Theory and Application of Length-Based Methods for

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Stock Assessment, 11–16 February 1985, Mazzara del Vallo, Sicily. *Edited by* D. Pauly and G.R. Morgan. International Center for Living Aquatic Resources Management, Manila and Kuwait Institute for Scientific Research, Safat. pp. 283–298. Available from www.worldfishcenter.org/libinfo/Pdf/Pub CP6 13.pdf [accessed 1 July 2006].

Sheehy, M.R.J. 1990. The potential of morphological lipofuscin age-pigment as an index of crustacean age. Mar. Biol. **107**(3): 439–442. doi:10.1007/BF01313426.

Sheehy, M.R.J. 1992. Lipofuscin age-pigment accumulation in the brains of ageing field- and laboratory-reared crayfish *Cherax quadricarinatus* (von Martens) (Decapoda: Parastacidae). J. Exp. Mar. Biol. Ecol. **161**(1): 79–89. doi:10.1016/0022-0981(92)90191-C.

Sheehy, M.R.J. 2001. Implications of protracted recruitment for perception of the spawner–recruit relationship. Can. J. Fish. Aquat. Sci. **58**(4): 641–644. Available from pubs.nrc-cnrc.gc.ca/cgi-bin/rp/rp2_abst_e?cjfas_f01-047_58_ns_nf_cjfas4-01 [accessed 1 July 2006].

Sheehy, M.R.J. 2002. A flow-cytometric method for neurolipofuscin quantification and comparison with existing histological and biochemical approaches. Arch. Gerontol. Geriat. **34**(3): 233–248. doi:10.1016/S0167-4943(01)00217-5.

Sheehy, M.R.J., and Bannister, R.C.A. 2002. Year-class detection reveals climatic modulation of settlement strength in the European lobster, *Homarus gammarus*. Can. J. Fish. Aquat. Sci. **59**: 1132–1143. doi:10.1139/F02-083.

Sheehy, M.R.J., and Prior, A.E. 2003. Analysis of stock age structure and population parameters in edible crab, *Cancer pagurus*, using lipofuscin age pigments: data for resource management. *In* Report of the Study Group on the biology and life history of crabs. Living Resources Committee, International Council for the Exploration of the Sea, Copenhagen. ICES CM 2003/G:11 Ref. D. pp. 40–42. Available from www.ices.dk/products/CMdocs/2003/G/G1103.PDF. [accessed 1 July 2006].

Sheehy, M.R.J., and Prior, A.E. 2005*a*. Update on neurolipofuscin demographic analysis of *Cancer pagurus* in the main English regional fisheries. *In* Report of the Study Group on the biology and life history of crabs. Living Resources Committee, International Council for the Exploration of the Sea. ICES CM 2005/G:10 Ref. D. pp. 56–58. Available from www.ices.dk/reports/LRC/2005/SGCRAB/sgcrab05.pdf [accessed 1 July 2006].

Sheehy, M.R.J., and Prior, A.E. 2005*b*. Analysis of stock age structure and population parameters in edible crab, *Cancer pagurus*, using lipofuscin age pigments: data for resource management. Marine Fisheries Research and Development Final Rep. MF0225. Department of Environment, Food and Rural Affairs, London, UK. Available from www.le.ac.uk/biology/mrjs2/MF0225.pdf [accessed 1 July 2006].

Sheehy, M.R.J., and Prior, A.E. 2007. Progress on an old question for stock assessment of the edible crab, *Cancer pagurus*. Mar. Ecol. Prog. Ser. In press.

Sheehy, M.R.J., and Shelton, P.M.J. 2001. Use of lipofuscin age pigment for age determination of lobsters. Marine Fisheries Research and Development Final Rep. MF0215/CSA 2596. Ministry of Agriculture Fisheries and Food, London, UK. Available from www.le.ac.uk/biology/mrjs2/MF0215.pdf [accessed 1 July 2006].

Sheehy, M.R.J., Greenwood, J.G., and Fielder, D.R. 1994. More accurate chronological age determination of crustaceans from the field using the physiological age marker, lipofuscin. Mar. Biol. **121**(2): 237–245. doi:10.1007/BF00346731.

Sheehy, M.R.J., Shelton, P.M.J., Wickins, J.F., Belchier, M., and Gaten, E. 1996. Ageing the European lobster *Homarus gammarus* by the lipofuscin in its eyestalk ganglia. Mar. Ecol. Prog. Ser. **143**: 99–111. Available from www.int-res.com/abstracts/meps/v143/p99–111/. [accessed 1 July 2006].

Sheehy, M.R.J., Caputi, N., Chubb, C., and Belchier, M. 1998. Use of lipofuscin for resolving cohorts of western rock lobster (*Panulirus cygnus*). Can. J. Fish. Aquat. Sci. **55**(4): 925–936. Available from pubs.nrc-cnrc.gc.ca/cgi-bin/rp/rp2_abst_e?cjfas_f98-016_55_ns_nf_cjfas55-98 [accessed 1 July 2006].

Sheehy, M.R.J., Bannister, R.C.A., Wickins, J.F., and Shelton, P.M.J. 1999. New perspectives on the growth and longevity of the European lobster (*Homarus gammarus*). Can. J. Fish. Aquat. Sci. **56**(10): 1904–1915. Available from pubs.nrc-cnrc.gc.ca/cgi-bin/rp/rp2_abst_e?cjfas_f99-116_56_ns_nf_cjfas [accessed 1 July 2006].

Sparre, P. 1990. Can we use traditional length-based fish stock assessment when growth is seasonal? Fishbyte, **8**: 29–32.

Sparre, P., and Venema, S.C. 1998. Introduction to tropical fish stock assessment. Part 1. Manual. United Nations Food and Agriculture Organization, Fish. Tech. Pap. No. 306/1, Rev.2. UN FAO, Rome. Available from www.fao.org/docrep/w5449e/w5449e00.htm [accessed 1 July 2006].

Szekely, M., and Szelenyi, Z. 2005. Regulation of energy balance by peptides: a review. Curr. Protein Pept. Sci. **6**(4): 327–353. doi:10.2174/1389203054546343.

Terman, A., and Brunk, U.T. 2004. Aging as a catabolic malfunction. Int. J. Biochem. Cell Biol. **36**(12): 2365–2375. doi:10.1016/j.biocel.2004.03.009.

Uglem, I., Bekhier, M., and Svasand, T. 2005. Age determination of European lobsters (*Homarus gammarus* L.) by histological quantification of lipofuscin. J. Crustac. Biol. **25**(1): 95–99. Available from www.bioone.org/perlserv/?request=get-abstract&doi=10.1651%2FC-2448 [accessed 1 July 2006].

Vetter, E.F. 1988. Estimation of natural mortality in fish stocks — a review. Fish. Bull. **86**(11): 25–43.

Vila, Y., Medina, A., Megina, C., Sobrino, I., and Ramos, F. 2000. Quantification of the age-pigment lipofuscin in brains of known-age, pond-reared prawns *Penaeus japonicus* (Crustacea, Decapoda). J. Exp. Zool. **286**(2): 120–130. doi:10.1002/(SICI)1097-010X(20000201)286:2<120::AID-JEZ3>3.0.CO;2-L.

Wahle, R.A., Tully, O., and O'Donovan, V. 1996. Lipofuscin as an indicator of age in crustaceans: analysis of the pigment in the American lobster *Homarus americanus*. Mar. Ecol. Prog. Ser. **138**: 117–123. Available from www.int-res.com/abstracts/meps/v138/p117-123/ [accessed 1 July 2006].

Woll, A.K., van der Meeren, G.I., and Fossen, I. 2006. Spatial variation in abundance and catch composition of *Cancer pagurus* in Norwegian waters: biological reasoning and implications for assessment. ICES J. Mar. Sci. **63**(3): 421–433. doi:10.1016/j.icesjms.2005.10.004.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Benjamin, S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Kimberley, A., Stachowicz, J.J., and Watson, R. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science (Washington, D.C.), **314**(5800): 787–790. doi:10.1126/science.1132294.

Zabel, R.W., and Levin, P.S. 2002. Simple assumptions on age composition lead to erroneous conclusions on the nature of density dependence in age-structured populations. Oecologia, **133**(3): 349–355. doi:10.1007/s00442-002-1051-0.

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An equilibrium model for predicting the efficacy of marine protected areas in coastal environments

Carl J. Walters, Ray Hilborn, and Richard Parrish

Abstract: Quantitative models of marine protected area (MPA) proposals can be used to compare outcomes given current biological knowledge. We used a model of a linear coastline, with 200 discrete cells each spanning 1.6 km of coast. This model is used to evaluate alternative proposals for marine protected area networks, predicting equilibrium changes in abundances and harvests while accounting for dispersal of larvae and older fish, changes in fecundity with reduced mortality in reserves, impacts of displaced fishing effort on abundances outside reserves, and compensatory (stock–recruitment) changes in postsettlement juvenile survival. The model demonstrates that modest dispersal rates of older fish can substantially reduce abundance within protected areas compared with predictions from models that ignore such dispersal. The strength of compensatory improvements in postsettlement juvenile survival is the most critical factor in determining whether a reserve network can rescue populations from the impacts of severe overharvesting. We use the model to compare specific alternative proposals for protected area networks along the California coast, as mandated through California's Marine Life Protection Act, and show that achieving the goals of the Act depends primarily on the fisheries management regulations outside of protected areas and that the size and configuration of MPAs has little impact.

Résumé : Des modèles quantitatifs des propositions de zones de protection marines (MPA) peuvent servir à comparer les résultats escomptés, compte tenu des connaissances biologiques actuelles. Nous utilisons un modèle comprenant une côte linéaire avec 200 cellules distinctes couvrant chacune 1,6 km de côte. Le modèle sert à évaluer des propositions de rechange pour un réseau de zones de protection marines en prédisant les changements des abondances et des récoltes à l'équilibre, tout en tenant compte de la dispersion des larves et des poissons plus âgés, du changement de fécondité relié à la diminution de la mortalité dans les réserves, des impacts sur l'abondance des efforts de pêche relocalisés hors des réserves et les changements compensatoires (stock–recrutement) de la survie des jeunes après leur établissement dans le milieu. Le modèle démontre que les taux de déplacement modestes des poissons plus âgés peuvent réduire considérablement les abondances dans les zones protégées, en contraste des prédictions des modèles qui ignorent ces déplacements. L'importance de l'amélioration compensatoire de la survie des jeunes après leur établissement est le facteur le plus critique pour déterminer si un réseau de réserves peut sauver une population des effets d'une récolte excessive. Nous utilisons le modèle pour comparer des propositions spécifiques de rechange de réseaux de zones de protection le long de la côte de la Californie, tel que requis par la loi californienne de protection de la vie marine (California Marine Life Protection Act), et nous démontrons que l'atteinte des objectifs de la loi dépend principalement des règlements de gestion des pêches à l'extérieur des zones de protection et que la taille et la configuration des MPA ont peu d'effet.

[Traduit par la Rédaction]

Introduction

A number of relatively simple, one-dimensional models have been proposed for evaluating population impacts of networks of marine protected areas (MPAs) distributed along coastal shorelines and extending offshore far enough to protect animals that undergo ontogenetic offshore movements (e.g., Botsford et al. 2004; Gaylord et al. 2005; Kaplan and Botsford 2005). The basic idea in these models has been to divide the shoreline into a large number of small (e.g., 1 km or 1 nautical mile (= 1.852 km)) spatial slices or cells, then predict changes in abundance within each of the cells. Typically, these models have accounted for linkage among cells through larval dispersal and for compensatory changes in juvenile survival rates after larval settlement. However, they have not accounted for dispersal of older animals or changes in fishing impacts in remaining open areas because of displacement of fishing effort out of reserve areas and (or) fisheries regulations aimed at reducing overall fishing mortality rates whether or not reserves are present. Models that do account for movement of older animals and spatial redistribution of fishing effort (Walters et al. 1999; Walters

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and Martell 2004; Hilborn et al. 2006) have led to much less optimistic predictions about the yield benefits of protected areas.

There is a need for relatively simple models that can be used to compare and screen alternative MPA proposals (differing in spacing and sizes of reserves) to give some idea of how different proposals will impact a range of species with widely different life histories, without resorting to very complex (and expensive to develop) models like Ecospace. The model of Hilborn et al. (2006) did not consider age structure or differential larval dispersal. Absent, simple, but realistic models, quantitative design guidelines, and proposals for MPA networks are liable to be based on intuitive guesses or simplistic percent target rules, and networks implemented on the basis of such guesses can have severe impact on fishing interests without achieving the intended conservation goals.

Here we propose a simple model that can be easily implemented using a spreadsheet, which accounts for dispersal of both larval and older fish, compensatory juvenile mortality, redistribution of fishing effort, and changes in mean fecundity of fish in protected areas due to accumulation of older, highly fecund individuals. We use the model to demonstrate for a range of indicator species that proposals for an MPA network along the California coast would very likely not meet intended conservation objectives unless accompanied by fisheries harvest management in remaining open areas that maintains biomass outside of reserves.

A key factor that has motivated our model development is that computer simulation studies (e.g., fig. 11.10 in Walters and Martell 2004; see also Meester et al. 2001) warn that impacts of heavy fishing pressure near MPA boundaries can have impacts on abundance that extend well into the MPA, beyond typical dispersal distances for the impacted species. Two mechanisms cause this effect: (*i*) individuals with home ranges near the boundaries are still subject to risk of harvest, and more importantly, (*ii*) dispersal imbalance effects, which have not been widely recognized by proponents of MPAs. Dispersal imbalance effects occur when there is movement out of sites near the boundary, which is not balanced by movements into the site because of lack of source animals from outside the MPA boundary. Models with density-dependent movement (more movement of individuals from high-density sites near the core of the MPA; see e.g., Abesamis and Russ 2005) predict even larger imbalance effects on overall MPA abundance. Such effects are difficult to measure in patchy environments and may take years to develop after a MPA is created, but can considerably reduce the long-term abundance benefits of localized protection from fishing.

California is the first state to plan an extensive series of marine protected areas under the legislation Marine Life Protection Act (MLPA). The MLPA mandates development of a network of marine reserves along the California coast, with basic goals of protecting marine communities and unique habitats. Planning for implementation of the Act's requirements has focused on the central coast area from Point Conception near Santa Barbara to Pigeon Point near Santa Cruz. A science advisory team has developed recommendations for MPA size and spacing based on review of movement and larval dispersal characteristics of a wide range of species, and these recommendations have been used to guide development of three alternative network proposals or plans (details and maps available at www.dfg.ca.gov/mrd/mlpa/centralcoast.html). Each of these proposals would protect 15%–20% of coastal areas from the impacts of at least demersal fishing.

A serious complicating factor in evaluation and comparison of these proposals is that the California Department of Fish and Game (with management responsibility for fisheries inside the state 3 mile limit (1 mile = 1.609 km)) and National Marine Fisheries Service (NMFS) (offshore species) have initiated extensive trawl and gill net fishing bans, species closures, large offshore closures for rockfish conservation, and protection of essential fish habitat, all aimed at rebuilding and sustainably managing a collection of species that have been classified as overfished. These species already being afforded management protection include red abalone (*Haliotis rufescens*), widow rockfish (*Sebastes entomelas*), bocaccio (*Sebastes paucispinis*), lingcod (*Ophiodon elongatus*), and inshore species like cabezon (*Scorpaenichthys marmoratus*). One of these, lingcod, has recently been declared by NMFS to be recovered.

Consequently the development of MPA proposal alternatives has taken place in an environment of extreme uncertainty. There is a need to account for high ecological complexity (species with a wide variety of life histories and dispersal characteristics); there is gross uncertainty about population parameters related to spatial processes (adult mortality and larval dispersal); and there is considerable uncertainty about the efficacy of other fisheries management measures. In such environments, and especially when a wide range of expertise and stakeholder interests are involved, even quite simple models can go a long way toward clarifying likely differences in outcomes among policy alternatives and in obtaining consensus about needs for adaptive management in implementation of the program (Walters 1997). Indeed, development of the model described below was motivated mainly by the possibility of using it in future adaptive management planning processes for the California coast.

In this paper, we construct a general model of a linear coastline broken into many small areas, as in Botsford et al. (2004), and use this model to evaluate specific proposals for the central coast of California proposed under the MLPA.

Materials and methods

When MPAs are to be placed along a coastline like California's, where each MPA is intended to protect an inshore–offshore band that includes both juvenile nursery and older fish residence areas, the most important population impacts of protection can be quantified by using a simple, one-dimensional spatial model with a large number of spatial cells or local sites that are linked through dispersal of both larvae and older animals. We develop the model by first providing an overall dynamic accounting and solution structure, then examine each element of that structure in more detail.

General dynamic structure and numerical solution method

We divide a coastline into $i = 1...n$ spatial cells, each extending a longshore distance of 1 mile and extending off-

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shore for an unspecified distance large enough to protect all life stages of a species. We assume initially that all of these cells are equally suitable for the species in terms of habitat conditions. If N_i is the number of older individuals in the cell (summed over all ages from an arbitrary age of recruitment or maturity), the dynamics of N_i can be approximated by the continuous recruitment–movement–mortality rate relationship:

$$(1) \qquad dN_i/dt = r(L_i) - MN_i - F_iN_i - 2mN_i + m(N_{i-1} + N_{i+1})$$

where $r(L_i)$ is local recruitment rate as a function of local larval settlement rate L_i, M is natural mortality rate, F_i is fishing and (or) bycatch mortality rate specific to cell i, m is movement rate of older animals out of cell i to the adjacent cells, and mN_{i-1} and mN_{i+1} are movement rates of animals into cell i from surrounding cells.

For evaluation of the long-term impacts of protection, we need not solve eq. 1 over time, and can instead try to find the long-term mean or equilibrium N_i implied by $dN/dt = 0$. This equilibrium abundance field must satisfy the relationship:

$$(2) \qquad N_i = [r(L_i) + m(N_{i-1} + N_{i+1})]/(M + F + 2m)$$

This is obtained just by setting dN/dt to zero and solving eq. 1 for N.) Owing to the nonlinear dependence of L_i and $r(L_i)$ on larval transport and survival patterns and on mean fecundity of the N_i in each cell, eq. 2 cannot be solved analytically for the long-term N_i; however, it can be easily solved by numerical relaxation methods. The simplest such method involves substituting successive estimates of L_i, N_{i-1}, and N_{i+1} into the right-hand side of eq. 2 and using the resulting estimates of N_i as the inputs for the next iterative substitution. However, that method converges very slowly.

The following procedure converges very rapidly (within 10–20 iterations) for most parameter combinations: (1) set N_i to the initial, trial values $N_i^{(1)}$ (e.g., $N_i^{(1)} = R_0/(M + F_0 + 2m)$, where R_0 is initial recruitment, and F_0 is initial fishing mortality rate; (2) use these estimates to solve eqs. 3–6 below for larval production, recruitment rates, and spatial F_i (setting F_i for closed areas to zero); (3) treating the resulting recruitment and F_i estimates as fixed constants, solve a tridiagonal equation system for equilibrium N_i, where each equation in the system is given by $r(L_i) = MN_i + F_iN_i + 2mN_i - m(N_{i-1} + N_{i+1})$. This results in a vector $N_i^{(eq)}$ of new N estimates; and (4) combine these with the previous estimates using a relaxation weight W of around 0.9 to give a next iterative estimate $N_i^{(2)} = WN_i^{(eq)} + (1 - W)N_i^{(1)}$. Then use these estimates in step 2 to begin another iteration, repeating steps 2–4 until the N_i estimates stop changing. Note that for each iteration, we calculate updated estimates of F_i under various hypotheses about redistribution of fishing effort and update the $r(L_i)$ function to represent changes in larval source abundances and mean fecundities.

Local recruitment dynamics

The really critical term in eqs. 1–2 is the recruitment function $r(L_i)$, which involves issues of both how far larvae are dispersed (how L_i is formed as a sum of larval contributions from other cells) and whether there is strong density dependence in postsettlement survival rates (whether or not juvenile nursery habitats are fully seeded so that recruitment is independent of larval settlement). In the absence of strong longshore advection of larvae in particular direction(s), we would expect dispersive mixing processes to result in a normally distributed pattern of larval settlement from spawning in each cell, with a spread or standard deviation parameter proportional to larval duration and mixing velocities per unit time. The normal distribution assumption for larval settlement implies that if there are no larval sources outside the study region, average L_i on each cell i should consist of a sum of larval contributions from potentially all other cells, with the functional form:

$$(3) \qquad L_i = k\sum_{j=1}^{n} \tilde{f}_j N_j e^{-0.5(i-j)^2/S^2}$$

Here, k is a scaling constant for total larval settlement from each source cell, S is the standard deviation of the spatial distribution of larval settlement (e.g., $S = 10$ implies that settlement of larvae produced in a cell drops off rapidly beyond 10 miles from that cell), and $\tilde{f}_j$ is mean relative fecundity of animals in cell j (see below; for simple simulations that ignore impact of harvesting on mean fecundity, set $\tilde{f}_j = 1.0$). Note that summing over all cells j implies that larval settlement on cell i may include contributions from any or all of the other cells j. The exponential term in eq. 3 results in a normally distributed pattern of larval settlement from each source cell, as would be expected if larval dispersal is essentially a random walk process without directional advection along the coast.

Using eq. 3 to predict average larval settlement to each cell i, the key issue then becomes prediction of how $r(L_i)$ varies with L_i. In the absence of evidence of recruitment suppression at high N_i due to cannibalism or spacing behaviors by the animals already present in cell i, we would expect the recruitment function to be of a saturating or Beverton–Holt form, i.e.,

$$(4) \qquad r(L_i) = \alpha L_i/(1 + \beta L_i)$$

where α is the maximum survival rate of larvae from settlement to recruitment, and α/β is the maximum recruitment rate (carrying capacity of the cell to produce recruits). We hypothesize a base or reference natural settlement rate L_0 for each cell, calculated by setting $k = 1$, $i = n/2$, and all N_j in eq. 3 to a base unfished abundance $N_j = R_0/M$, where R_0 is an average natural recruitment rate per cell. Then we can parameterize the recruitment relationship in terms of R_0, L_0, and the Goodyear compensation ratio (K, ratio of maximum larval survival at low densities to survival at unfished natural abundance) by setting

$$(5) \qquad \alpha = KR_0/L_0$$

$$\beta = (K - 1)/L_0$$

Note that in this parameterization of the Beverton–Holt function, absolute larval production per spawner (k) does not matter, since only the product $k\alpha$ actually appears in the recruitment prediction. Meta-analyses of stock–recruitment data indicate that we should expect K to be in the range 5–100 (see e.g., Goodwin et al. 2006), with most likely values for long-lived benthic species in the range $K = 10$–50. The

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critical parameter in this representation is K, which determines how much larval settlement can be reduced before net recruitment $r(L_c)$ is impaired; R_o is simply a scaling parameter that is determined by (or implies or represents) the units of measurement of N_i.

In assuming that local recruitment depends only on local larval settlement (eq. 4), we join other modelers (e.g., Botsford et al. 2004; Gaylord et al. 2005; Kaplan and Botsford 2005) in ignoring postsettlement, longshore movement by juveniles prior to recruitment to the older population N. This is not a serious issue for species where juvenile nursery habitat is widely distributed along the coast, since for such species, juvenile movement just acts like wider spreading of larvae in the first place (we could account for it by increasing S in eq. 3). But for species that depend on very restrictive nursery habitats (e.g., estuaries) from which juveniles fan out to occupy other habitats as part of their ontogeny, we really should include calculations of prerecruit juvenile movement using the same approach as eq. 3 but applied to the survivors from density-dependent mortality effects in the restricted nursery areas.

The above formulation allows for variation among species in the following basic life history parameters: M, natural longevity (annual natural mortality rate); m, adult diffusive movement rate between cells (per year); F, base (and policy) fishing mortality rate (per year); S, larval dispersal distance (standard deviation of normal settlement curve, miles); K, compensatory improvement in juvenile survival at low stock sizes. The only major population dynamics factors that are not represented in the above equation system are (*i*) changes in mean larval production per adult with changes in age–size composition (i.e., increases in mean fecundity f_i per N_i in spatial cells that have lower total mortality rates $M + F_i$ and (*ii*) spatial variations in juvenile and adult habitat capacity, as might be reflected in spatial variation in the juvenile carrying capacity parameter β and in adult dispersal rate m (i.e., higher dispersal rates out of areas with relatively poor habitat). It is not difficult to model spatial variation in mean fecundity with variation in $M + F_i$ for species that are not highly dispersive (low movement rates m). Omitting this variation results in somewhat conservative predictions about the benefits to larval production of reducing local mortality rates (when dispersal rates are high, mean fecundity cannot increase in protected areas, since loss of older animals into fished areas prevents the development of a natural age structure; only relatively small (e.g., 5%), annual emigration rates are enough to substantially lower mean fecundity for long-lived species). We have tested a simple method for representing variable fecundity, assuming f_i is proportional to a power of the ratio of numbers per recruit to unfished numbers per recruit (see below), and found no substantial change in the basic predictions. It is likewise simple to model variation in nursery capacities (β) among cells and m.

For simple policy-screening exercises involving general comparisons of how well alternative MPA proposals are likely to perform at enhancing abundances of animals with a range of different life histories (M, m, S, F, K values), it is probably best not to complicate the comparisons by including variations in spatial habitat and effects of increased longevity–fecundity. In simple game-playing exercises where we have varied the life history parameters widely, we have found that predictions are typically not particularly sensitive to the M and S parameters. The parameter m determines the extent to which there will be substantial increases in biomass inside reserves. For longer-lived species ($M <$ 0.2), the reserve must be greater than 5–10 times the mean dispersal distance to lead to major increases inside reserves. The most critical parameters for predicting the overall outcome are the parameters F and K. These are exactly the same parameters that are most critical in comparisons of fisheries harvesting policies in general, using standard stock assessment models.

Spatial variation in fishing effort

When using the model to evaluate MPA proposals that involve closing a large proportion of the cells to fishing (by setting F_i for those cells to zero or to some lower predicted poaching rate), a key consideration is what to assume about fishing effort displaced from the cells after closure. One simple option is to assume historical F_o, which amounts to assuming that total fishing effort will be reduced so that the F_i in each remaining cell does not increase. A more realistic option is to assume that displaced effort is spread across the remaining open cells, so that F_i for each cell changes from a base value F_o to a higher value $F_i = F_o/(1 - c)$, where c is the proportion of the cells closed to fishing under the proposal. A still more realistic option is to use a gravity or multinomial logit model to predict spatial redistribution of fishing effort, so as to recognize likely concentration of fishing effort near MPA boundaries where abundances are enhanced by spillover effects of m.

Spatial variation in fishing effort can be predicted with a multinomial logit (gravity model) based on the assumption that the average utility of each area to fishers is proportional to the logarithm of abundance in that area. This leads to the spatial effort or fishing mortality allocation model:

$$(6) \qquad F_i = F_{total} N_i^{1/v} C_i / \Sigma_j N_j^{1/v} C_j$$

Here v is a standard deviation among fishers in perception of the utility of fishing in cell i compared with other areas (higher v spreads effort more evenly along the coast), F_{total} is the total number of spatial cells times the base assumed fishing rate F_o per cell, and C_i is set to 1.0 for cells that are open to fishing and to 0 for closed cells.

Spatial variation in habitat quality

Habitat quality for both juveniles and older fish of any species is likely to vary considerably along any large coastline. Spatial variations in habitat quality or carrying capacity among cells can be represented by variation in dispersal rates and recruitment carrying capacities. For each cell, assume that relative habitat quality can be represented by a 0–1 index value h_i, where $h_i = 1$ represents the best quality habitat and $h_i = 0$ represents completely unsuitable habitat. A simple way to estimate h_i is to examine distributions of fishing effort prior to establishment of reserves, since effort is likely to be concentrated in cells with higher habitat quality and fish abundance. Then we simply multiply the recruitment α for each cell by h_i in predicting recruitment and further assume that emigration rates (m out of the cell) in-

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crease to m/h_i for cells with low h_i, while immigration rates (m into the cell) decrease to h_i/m for cells with low h_i.

Changes in mean fecundity

Spatial variation in $\bar{f}_i$ can be represented by estimating the equilibrium size–age structure of each cell and adjusting that cell's contribution to total larval production accordingly. It has been pointed out (e.g., Gaylord et al. 2005) that protected areas will allow buildup of older, more fecund animals, and these animals will make disproportionate contributions to total larval production. Fish typically mature at about 8%–10% of their maximum body weight, and fecundity is typically proportional to body weight above the weight at maturity. For slow-growing species like widow rockfish, such growth–fecundity patterns result in age–fecundity patterns like that shown in Fig. 1.

When a long-lived stock is heavily exploited, such an age–fecundity pattern can obviously lead to large decreases in mean fecundity when mean age is severely reduced by fishing. For example, if widow rockfish were exploited at an annual exploitation rate of 25% at ages 4 and older for long enough so that the population age structure could stabilize, the annual egg production per recruit in the exploited (age 4+) population would drop from around 6.6 eggs per recruit (relative scale) for an unfished population to only 0.5 eggs per recruit under harvesting. This implies a drop in relative mean fecundity per age 4 and older animal from 0.05 to only 0.01 (in this calculation, eggs per recruit is calculated as survivorship to age times fecundity at age, and eggs per fish is eggs per recruit divided by numbers of fish present per recruit).

Based on calculations like these, we might expect a gain of as much as fivefold in mean egg production by fish resident in MPAs. Unfortunately, such gains can only be expected for completely sedentary species. It is not difficult to calculate the equilibrium age structure for each spatial cell along a coast by numerically integrating the die-off rate equation for a typical cohort in each cell i:

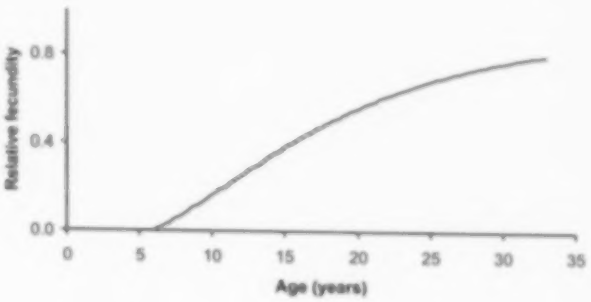
$$(7) \qquad dN_i/dt = -(M + F_i + 2m)N_i + m(N_{i+1} + N_{i-1})$$

Note that this equation includes a dispersal loss term, $2mN_i$, representing dispersal to other cells, and a gain term, $m(N_{i+1} + N_{i-1})$, for immigration of animals (of the same age) from surrounding cells. Because of the cross-cell linkage and possibility of highly variable F_i among cells i, eq. 7 has to be integrated using very short time steps (0.25 years or less), along with some iterative method for estimating the mean of the gain term $m(N_{i+1} + N_{i-1})$ over each integration time step. But an important point about eq. 7 is that each cohort within cell i suffers a loss rate of $2mN_i$ to adjacent cells, which may or may not be balanced by immigration from those cells, even when $F_i = 0$. Thus, it can be seriously incorrect, especially for small MPAs and animals with high m values, to assume that unfished cells will reach the unfished equilibrium age structure predicted by the natural stock decay equation $dN_i/dt = -MN_i$ for a typical cohort in the absence of fishing and movement.

Assessment of m of older fish

The instantaneous movement rate m of older fish in eq. 1 can obviously have a large impact on predictions of N_i. Note that if the spatial cells are of unit long-shore width, the sum of terms $-2mN_i + m(N_{i+1} - N_{i-1})$ in eq. 1 is a discrete approximation of the diffusion term $D\partial^2 N dx^2$ that appears in continuous one-dimensional (x) spatial models for movement treated as a random walk process (Okubo 1980). That is, m is the same as the diffusion coefficient usually called D in such models.

Fig. 1. Age–fecundity relationship for widow rockfish (*Sebastes entomelas*), assuming von Bertalanffy $K = 0.1$ and maturity at 9% of maximum body weight.



A useful mathematical result about such random diffusion processes is that if a set of animals are tagged at some point in space and then allowed to move for some time t (e.g., 1 year), their distribution is expected to be normal with position mean 0 (no net advection along shore) and variance $2Dt = 2mt$ (Goel and Richter-Dyn 1974). So if there are tagging data that provide a distribution of annual ($t = 1$) movement distances, the standard deviation S of this distribution (a measure of average movement distance) is an estimate of $(2m)^{1/2}$ (i.e., $m \approx S^2/2$).

The m parameter is not a discrete-time movement proportion and hence can have very large values. The total dispersal loss across any cell boundary from cell i is predicted to be mN_i, and for highly mobile animals this flux can obviously be many times the number of animals N_i present in the cell at any moment.

For relatively sedentary species with distinct home ranges, distributions of movement distances are likely to show two distinct patterns, with many animals showing apparently zero movement and others showing relatively large movements. In such cases, it is tempting but incorrect to think of m as consisting of the product of two factors: a probability of moving at all multiplied by half the square of the mean distance moved for those individuals that do disperse. Suppose instead that N_i is viewed as divided at any moment into two behavioral types of animals: S_i sedentary individuals and D_i actively dispersing individuals ($N_i = S_i + D_i$). The rate dynamics of these components can be represented by the pair of equations (where $Z = F + M$)

$$(8) \qquad dS_i/dt = r(L_i) - Z_i S_i - eS_i + sD_i$$

$$dD_i/dt = eS_i - Z_i D_i - sD_i - 2mD_i + m(D_{i+1} + D_{i-1})$$

Here, e represents the (relatively low) movement rate of animals from sedentary to dispersive state, and s represents the

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Table 1. Simple model parameters for five test species found along the California coast.

Simple model parameters	Red abalone	Widow rockfish	Lingcod	Bocaccio	Cabezon
Base recruitment (R_o)	1	1	1	1	1
Annual adult mortality (M)	0.1	0.125	0.25	0.15	0.3
Fishing mortality rate (F)	0.08	0.06	0.25	0.056	0.2
Adult emigration rate (~miles·year^{-1})[a]	0.01	0.5	6	6	1.5
Larvae per adult (k)	100	100	100	100	100
Goodyear compensation ratio (K)	3	20	10	4	10
Larval transport distance parameter (S)	0.3	40	15	45	1.5

Note: Red abalone (*Haliotis rufescens*), widow rockfish (*Sebastes entomelas*), lingcod (*Ophiodon elongatus*), bocaccio (*Sebastes paucispinis*), cabezon (*Scorpaenichthys marmoratus*).
[a]1 mile = 1.609 km.

(likely very high) movement rate of dispersing animals back into the sedentary state. The equilibria of these equations ($S_i = [r(L_i) + sD_i]/(Z_i + e)$ and $D_i = [eS_i + m(D_{i+1} + D_{i-1})]/(Z_i + s + 2m)$, respectively) can be found by the same iterative procedures as described above for N_i. We have found that these solutions are very close to those of the simpler diffusive model with $m = e$, that is the slow rate of movement into the dispersive state dominates the effective value of m for the population as a whole.

For animals that have relatively large home ranges but rarely disperse (very low e in eq. 8), another alternative to treating movement as dispersive is to assume no dispersive movement at all, but to account instead for partial exposure of N_i to fishing mortality rates in other spatial cells. In this formulation, it is necessary to calculate F_i, which now needs to be defined as the effective fishing mortality rate suffered by animals whose home ranges are centered in cell i, as a sum of proportions of time that cell i animals spend in surrounding cells multiplied by effort-based fishing mortality risks for each of those cells. This results in the same qualitative effect as dispersal imbalance near the border of protected areas, namely depression in abundance for spatial cells near such borders. However, just how far that depressing effect extends into a multicell MPA depends on the details of how much time animals are assumed to spend in cells surrounding the center of their home ranges.

Results

We used the model to examine how the five historically overfished indicator species mentioned above might respond under the three alternative proposals for the central coast study area. To do this, we first obtained rough estimates of the model parameters for each species (Table 1) from information in stock assessment documents and from syntheses of information by the California science advisory team. Then we divided the central coast study region into 200 spatial cells, each roughly 1 mile wide. Using maps of the proposed closures, we designated each cell as closed ($F_i = 0$) or open ($F_i > 0$) to fishing for each of the proposals; all of the test species are benthic, so we made no distinction between types of protected area (e.g., we ignored the fact that some MPAs would be open to fishing for pelagic species). Only a few of the proposed MPAs extend offshore far enough to fully protect the rockfishes, but we assumed for those proposed MPAs that coordination of state and federal protective measures will eventually lead to permanent offshore, as well as inshore, protection; at present, federal regulations have nearly shut down demersal fishing offshore of all the proposed MPAs as rockfish conservation areas and (or) essential fish habitat closures.

In relation to uncertainty about future fisheries management, we examined two alternative scenarios for future fishing mortality rates in areas remaining open to fishing: one where management target Fs are met through the current conservative regulations and one where regulation fails and much higher Fs (e.g., 0.2 for rockfish) prevail in open areas. We did not model possible enforcement failures within MPAs, a particular concern for red abalone, where very high prices and easy access to shallow waters have likely created severe poaching problems.

We evaluated three specific proposals considered in the MLPA process, known as package 1, package 2, and package 3R. Package 3R formed the basis of the final recommendation, and there was considerable disagreement among stakeholders as to the costs and benefits of these three packages.

Sample results are shown from integrating eq. 7 (Fig. 2*a*), then calculating average fecundity per animal from the age–fecundity relationship in Fig. 1 for a species with growth and mortality characteristics similar to widow rockfish and a relatively low annual movement rate of $m = 0.5$ (roughly, 0.5 miles per year) under package 3R. Peaks in mean fecundity occur where there are protected areas (using California coast proposals as example; see below). But we see from this example that predicted mean fecundity per age 4 and older fish only approaches the unfished fecundity mean near the center of the largest MPA (off Vandenberg Air Base, California). When we repeat the calculations assuming a lower fishing mortality rate, $F = 0.07$, near the current Pacific Fisheries Management Council target for long-term management, we obtain the pattern shown in the portion of the panel labeled management. Even in this far more sustainable scenario, mean fecundity is reduced considerably in most areas from the natural baseline and again only approaches it in the largest MPA. Peaks in mean fecundity are predicted to occur in proposed protected areas, but mean fecundity only reaches the expected value for an unfished stock near the center of the largest proposed MPA (off Vandenberg Air Base, approximately 16 km wide MPA).

The approximate mean fecundity lines in Fig. 2 (dashed) are those obtained by predicting mean fecundity as $(N_i/N_o)^F$, where N_i/N_o is the ratio of equilibrium numbers per recruit to numbers per recruit in an unfished population, with the

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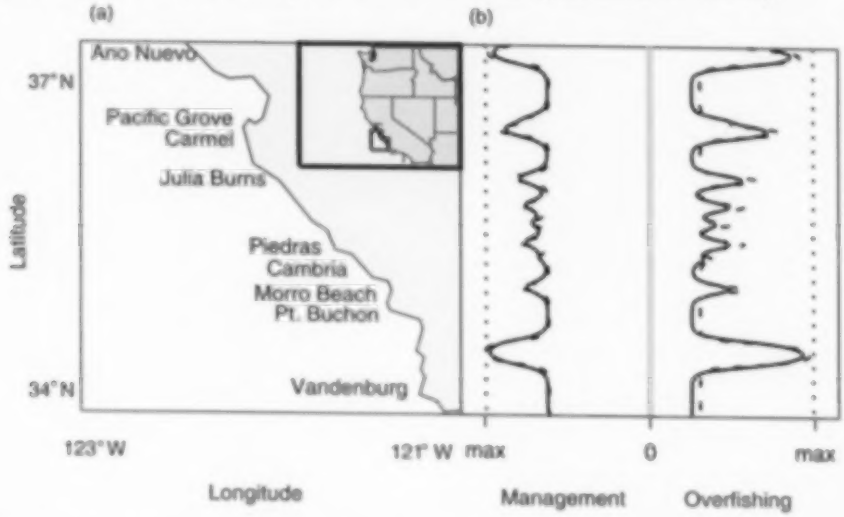
Fig. 2. Predicted spatial variation in mean fecundity for a species like widow rockfish (*Sebastes entomelas*) (mean adult dispersal distance 0.8 km·year^{-1}, $M = 0.1$, vulnerable to fishing at age 4), measured along the California coast southward from San Francisco Bay to Cape Conception. (*a*) The coastline with some locations labeled (inset shows location on US west coast). (*b*) Mean fecundity over space for two scenarios: one with high fishing mortality rate ($F = 0.25$) outside marine protected areas (MPAs) and one with much lower rate ($F = 0.07$) proposed for long-term management by Pacific Fisheries Management Council. Dotted lines indicate mean fecundity in the absence of any fishing, solid lines are predicted mean fecundity, and dashed lines are the approximate mean fecundity.



empirical power parameter $p = 1.3$. As noted above, this approximation was used to model spatially variable fecundity in some runs of the simple model and made essentially no difference to the overall patterns predicted by the model.

The result of the mean fecundity analysis is that gains in population viability due to survival of animals to older, more fecund ages can be expected only for species that are highly sedentary and subject to high, uncontrolled exploitation rates outside MPAs. Planners should not expect such gains from most fish species in coastal ecosystems.

Basic results of the simplest analysis (with no spatial variation in habitat quality, fishing effort concentrated near MPA boundaries) show that except for completely sedentary species like red abalone, widespread restoration to productive stock sizes is unlikely to be achieved through any of the MPA proposals unless accompanied by successful fisheries management (achievement of relatively low Fs) in open areas (Fig. 3). The model predicts that a fundamental weakness in all of the proposals is that the MPAs are too small (most are 5–10 km longshore) to protect species with even relatively low ($m = 1$) movement rates of older animals. For these species, dispersal imbalance effects lead to reduced abundances (and mean fecundities) all the way to the centers of all but the largest (off Vandenberg Air Base, for package 1) MPAs that were proposed. The dispersal imbalance effects lead in turn to much lower predictions of total larval production than would be expected if $m = 0$, and that lower larval production leads in turn to persistence of recruitment overfishing effects if stocks outside MPAs remain depleted. We found that there were reasonably small differences in yield or total abundance among the three packages, that yield was generally higher without any MPAs in place, and that the abundance and yield depended primarily on the fisheries regulations outside of MPAs.

We ran a wide variety of sensitivity tests on the predictions, varying particularly the adult movement parameter m and including spatial variation in habitat quality with the h_i estimated by examining areas of concentration of fishing effort (assuming effort tends to concentrate in areas where good habitat has led to fish concentrations). The tests on m show that basically the same results as shown in Fig. 3 can be expected for fish species with $m > 0.5$ (i.e., for fish species that move on average more than about 0.5 mile per year). The different life histories and different MPA packages examined serve as large-scale sensitivity tests for the basic biological and regulatory parameters.

Adding complex longshore habitat structure to the analysis (Fig. 3*f*) leads to a much more complex spatial pattern, but still about the same differences among policies as for the flat world scenarios (other panels of Fig. 3). However, because of the heavy bias towards hard-bottom habitat in each of the MPA proposals, it does result in larger increases in total abundance with all of the MPA proposals. The percentage of hard-bottom habitat inside MPAs with the variable habitat model (36.8%–47.8%) is more than twice the nominal percentage (14.9%–19.3%) in the constant habitat model.

It appears that there will be negative consequences for fishery yields under all the MPA packages if other fisheries management measures are successful (Table 2). We calculated equilibrium total catch for each proposal simply by summing $F_i N_i$ over all spatial cells for the model case where there is spatial variation in habitat quality (as in Fig. 3) and where fishery management is successful at achieving the target fishing rates in Table 1. In that case, MPAs simply concentrate fishing so as to reduce N_i and catch per effort in open areas relative to what it would be if all cells were well managed, and this reduction in CPUE leads to considerable loss in total yield and in lower overall Fs than intended.

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Fig. 3. Predicted equilibrium patterns of relative abundance for a selection of indictor species, calculated using the spatial model with constant habitat quality. The *y* axis of the each graph is geographic position, from just below San Francisco Bay at the top to Point Conception at the bottom. Each panel has the abundance in a management scenario and an overfished scenario; higher values of the management scenario are to the left, higher values of the overfished scenario are to the right. The dashed lines represent abundance in the absence of fishing, solid lines represent abundance with marine protected areas (MPAs), and dotted lines represent abundance with fishing but no MPA. Abundance is measured in relative (per recruit) units. Note that predicted abundances drop off near the range limits because of not accounting for dispersal of larvae and older animals into the modeled area from outside regions, while accounting for dispersal losses to those regions. Parameter values for simulations are as shown in Table 1 (except that fishing rates for red abalone (*Haliotis rufescens*) and widow rockfish (*Sebastes entomelas*) are set to 0.3 to simulate high historical fishing impact). Panel *f* represents predicted spatial distributions for bocaccio (*Sebastes paucispinis*); model including spatial habitat variation is assumed to be correlated with spatial distribution of fishing effort. Lingcod (*Ophiodon elongatus*), cabezon (*Scorpaenichthys marmoratus*).

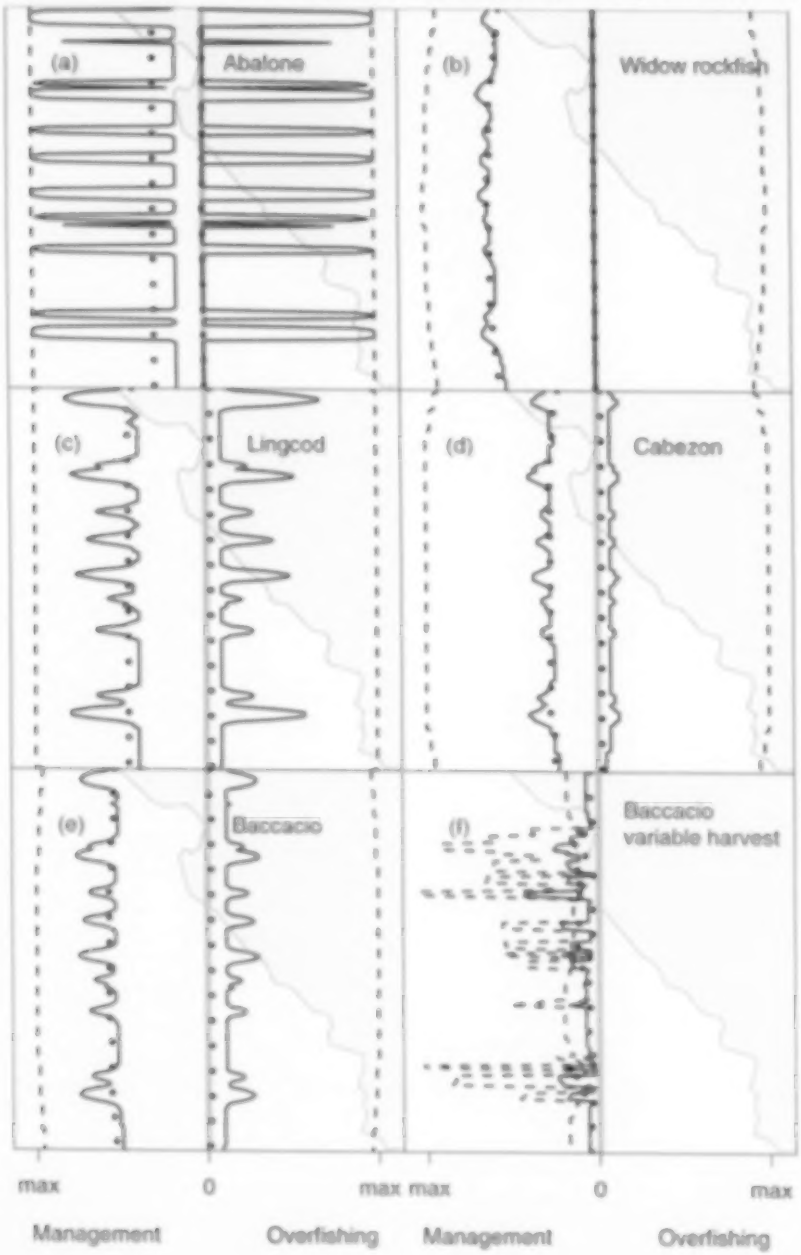

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Table 2. Equilibrium relative abundances and yields predicted by the simple spatial model, with variable habitat quality (correlated with historical fishing effort concentrations) and fishing effort responses to spatial variation in abundances.

	Red abalone	Widow rockfish	Lingcod	Bocaccio	Cabezon
Abundance					
Without fishing	683.8	637.8	296.8	474.1	249.2
Without MPAs	205.0	293.1	72.2	232.2	100.2
Package 1	293.4	323.2	99.4	253.0	119.7
Package 3R	317.2	322.6	95.0	258.1	122.5
Package 2	329.6	319.9	92.9	256.3	122.8
Catch					
Without fishing	0.0	0.0	0.0	0.0	0.0
Without MPAs	21.1	32.2	25.1	20.8	27.4
Package 1	13.1	30.0	25.2	19.5	23.1
Package 3R	11.2	30.2	26.3	19.5	23.7
Package 2	10.3	30.4	26.2	19.6	23.5
Fishing mortality (F)					
Without fishing	0.00	0.00	0.00	0.00	0.00
Without MPAs	0.10	0.11	0.35	0.09	0.27
Package 1	0.04	0.09	0.25	0.08	0.19
Package 3R	0.04	0.09	0.28	0.08	0.19
Package 2	0.03	0.10	0.28	0.08	0.19

Note: Note that values for "Without MPAs" (marine protected areas) option are predicted using current fisheries management policy (i.e., assuming that current fishing mortality rate goals are met by other means than protected areas). Red abalone (*Haliotis rufescens*), widow rockfish (*Sebastes entomelas*), lingcod (*Ophiodon elongatus*), bocaccio (*Sebastes paucispinis*), cabezon (*Scorpaenichthys marmoratus*).

A matter of considerable concern in scientific discussions of the California proposals has apparently been larval dispersal distances, with planning documents mentioning the need for MPA spacing that will allow for connectivity in larval settlement among reserves. The model indicates that if overfishing does persist outside reserves, roughly 40%–50% of larval settlement will eventually be from fish resident in reserves because of even modest buildup in abundances and mean fecundities. Further, this prediction is largely insensitive to assumed average larval transport distances (S parameter), except for species like red abalone or cabezon that have extremely short larval dispersal distances.

Discussion

The results shown here are very discouraging from the perspective of using MPAs as a tool for fish stock and ecosystem restoration and are very similar to the relatively pessimistic results obtained with much more complex models like Ecospace. MPAs of the size and spacing proposed for the hallmark California case will only offer substantial protection to a very small proportion of marine fish and invertebrate species, making up only a small percentage of the biomass and production of that coastal ecosystem (see Field et al. 2006 for a review of biomass distributions across the California Current ecosystem).

The scenarios in Fig. 3 indicate that monitoring programs could expect to see substantial increases in abundance within MPAs relative to surrounding fished areas, as has now been widely observed in studies of MPA performance (Halpern and Warner 2002). The basic problem is that inside–outside abundance comparisons do not involve a sound baseline (i.e., do not reveal how much more abundant some species could or should be if widely protected). In short, it is meaningless to show that some species is twice as abundant within an MPA than outside, if even the inside abundance is only a tiny percentage of the unharvested population size. For most species in most places, there is little recourse but to use population dynamics models, with attendant uncertainty about parameter values, to establish such baselines or performance reference points.

Equilibrium spatial models can be solved quickly for policy screening and tests of sensitivity to parameters, but they do not give any indication of how long MPA effects might take to develop (a key issue in adaptive management planning). They can serve the same role in protected area planning as do equilibrium yield-per-recruit models in fisheries harvest policy analysis: to give a sense of the best long-term settings for policy variables (like age at first capture) without specifying how such settings might be implemented. But after first screening for policies that make long-term sense, it is usually relatively easy to develop more detailed models to examine time patterns and other possible pitfalls in the equilibrium calculations.

It would be foolish to claim that such equilibrium models can be precisely parameterized by fitting to field data, as we would do with ordinary stock assessment models. While such exercises might reveal some basic patterns such as variation in habitat quality h_i, they do not represent a wide variety of fine-scale processes that shape fish distributions in time and space. To capture all of these processes via some model-fitting procedure would require a much more complex parameterization with all sorts of nuisance parameters (for factors like historical recruitment variability) that are

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not likely in fact to be critical for average, long-term policy performance. While we will doubtless move in the direction of such realistic models to understand some fine-scale processes, it is important to develop simpler models as policy-screening tools.

It would seem that for species that have been severely reduced by historical fishing, particularly those that have life history ontogeny involving inshore nursery areas and later movement into deeper waters, there is the possibility that nursery areas are now widely underseeded with larvae (i.e., are not producing nearly as many offshore recruits as they could). If this is the case, then even onshore–offshore protection (MPAs that extend well offshore) will not insure rapid population recovery, since abundance even in the MPAs may be limited by inadequate recruitment rather than depressed survival. For such species, the main connectivity among MPAs will be due mainly to relatively large-scale larval dispersal rather than to along-shore movement of older fishes. But if even larval settlement into MPAs is depressed because of large-scale historical overfishing, then recovery in MPAs will be slow enough that (unless a very high proportion of the offshore population is protected) most larval settlement will have to come from spawning outside the MPAs. That is, it may be wrong to suppose that MPA spawning abundances will recover rapidly so as to provide widespread larval seeding including connection through larval transport with other MPAs.

Our results are consistent with Allison et al. (1998), who found that protected areas are not sufficient to assure conservation of marine species. However, our results show that protected areas are also not necessary, stocks can be rebuilt and maintained by reducing fishing mortality rates alone, and none of the biology in the model we used suggests protected areas provide additional benefits to abundance and yield.

The model we present, or similar models that include spatial structure of populations, adult and larval dispersal, and the spatial allocation of fishing effort in response to changes in abundance, are straightforward to implement and can be used to quantitatively evaluate alternative MPA proposals. While such models are dependent upon specific assumptions, particularly dispersal assumptions, such models should be used when alternative MPA designs are being evaluated.

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References

Abesamis, R.A., and Russ, G.R. 2005. Density-dependent spillover from a marine reserve: long-term evidence. Ecol. Appl. **15**: 1798–1812.

Allison, G.W., Lubchenco, J., and Carr, M.H. 1998. Marine reserves are necessary but not sufficient for marine conservation. Ecol. Appl. **8**(Suppl.): S79–S92.

Botsford, L.W., Kaplan, D.M., and Hastings, A. 2004. Sustainability and yield in marine reserve policy. Am. Fish. Soc. Symp. **42**: 75–86.

Field, J.C., Francis, R.C., and Aydin, K. 2006. Top-down modeling and bottom-up dynamics: linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. Progr. Oceanogr. **68**: 238–270.

Gaylord, B., Gaines, S.D., Siegel, D.A., and Carr, M.H. 2005. Marine reserves exploit population structure and life history in potentially improving fisheries. Ecol. Appl. **15**: 2180–2191.

Goel, N.S., and Richter-Dyn, N. 1974. Stochastic models in biology. Academic Press, New York.

Goodwin, N.B., Grant, A., Perry, A.L., Dulvy, N.K., and Reynolds, J.D. 2006. Life history correlates of density-dependent recruitment in marine fishes. Can. J. Fish. Aquat. Sci. **63**: 494–509.

Halpern, B.S., and Warner, R.R. 2002. Marine reserves have rapid and lasting effects. Ecol. Lett. **5**: 361–366.

Hilborn, R., Micheli, F., and DeLeo, G. 2006. Integrating marine protected areas with catch regulation. Can. J. Fish. Aquat. Sci. **63**: 642–649.

Kaplan, D.M., and Botsford, L.W. 2005. Effects of variability in spacing of coastal marine reserves on fisheries yield and sustainability. Can. J. Fish. Aquat. Sci. **62**: 905–912.

Meester, G.A., Ault, J.S., Smith, S.G., and Mehrotra, A. 2001. An integrated simulation modeling and operations research approach to spatial management decision making. Sarsia, **86**: 543–558.

Okubo, A. 1980. Diffusion and ecological problems: mathematical models. Springer-Verlag, New York.

Walters, C. 1997. Challenges in adaptive management of riparian and coastal ecosystems. Conserv. Ecol. **1**(2): 1. [online]. Available from www.consecol.org/vol1/iss2/art1/.

Walters, C.J., and Martell, S.R. 2004. Fisheries ecology and management. Princeton University Press, Princeton, N.J.

Walters, C.J., Christensen, V., and Pauly, D. 1999. Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems, **2**: 539–544.

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Estimating abundance of pelagic fishes using gillnet catch data in data-limited fisheries: a Bayesian approach

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Abstract: We describe a Bayesian modelling approach to estimate abundance and biomass of pelagic fishes from gillnet catches in data-limited situations. By making a number of simple assumptions, we use fish sustained swimming speed to calculate the effective area fished by a gillnet in a specified soak time to estimate abundance (fish·km^{-2}) from the number of fish caught. We used catch data from various sampling methods in northern Australia and elicited anecdotal information from experts to build a size distribution of the true population to compensate for size classes that were unlikely to be represented in the catch because of size selectivity of the gear. Our final abundance estimates for various-sized scombrids (0.04–4.17 fish·km^{-2}) and istiophorids (0.004–0.005 fish·km^{-2}) were similar to what has been estimated for similar species in more data-rich situations in tropical regions of the Pacific Ocean. The model is particularly useful in data-limited situations in which abundance or biomass estimates are required for pelagic fish species of low economic importance. These data are often required for ecosystem models (e.g., Ecopath) that are increasingly being considered as potential tools for ecosystem-based fisheries management.

Résumé : Nous présentons une méthodologie de modélisation de type bayésien pour estimer l'abondance et la biomasse de poissons pélagiques à partir de récoltes au filet maillant lorsque les données sont limitées. En faisant quelques présuppositions simples, nous utilisons la vitesse de nage soutenue des poissons pour estimer la surface effective de capture d'un filet maillant durant une période donnée de mise en eau afin d'obtenir une estimation de l'abondance (poissons·km^{-2}) d'après le nombre de poissons capturés. Nous avons utilisé des données de capture par différentes méthodes d'échantillonnage dans le nord de l'Australie et nous avons recueilli des renseignements anecdotiques chez des experts afin d'élaborer une distribution en taille de la population véritable pour compenser l'absence des classes de taille qui risquent de ne pas être représentées à cause de la sélectivité des engins de pêche. Nos estimations finales d'abondance pour les scombridés (0,04–4,17 poissons·km^{-2}) et les istiophoridés (0,004–0,005 poisson·km^{-2}) de diverses tailles sont semblables aux estimations faites pour des espèces semblables des régions tropicales du Pacifique dans des situations où les données étaient plus nombreuses. Notre modèle est particulièrement utile lorsqu'on veut obtenir des estimations d'abondance ou de biomasse d'espèces de poissons pélagiques de faible importance économique et pour lesquelles on possède peu de données. Ces informations sont souvent requises dans les modèles d'écosystèmes (par ex., Ecopath) qui sont de plus en plus vus comme des outils potentiels dans la gestion des pêches axée sur les écosystèmes.

[Traduit par la Rédaction]

Introduction

Pelagic fishes such as tunas, mackerels, and billfishes support some of the most valuable commercial and recreational fisheries worldwide (Food and Agriculture Organization of the United Nations 2005). Moreover, these species are ecologically important as they are often high-order or apex predators that can strongly influence pelagic ecosystem structure (Olson and Boggs 1986; Myers and Worm 2003). A critical requirement for understanding the dynamics of pelagic fish populations is to have knowledge of their abundance or biomass. Not only is this information important for stock assessment to manage commercially important species, but in recent years, this type of information has become increasingly important for ecosystem models (Christensen and Pauly 1992). These ecosystem models are being used more widely with the growing interest worldwide in ecosystem-based approaches to fisheries management (Hall and Mainprize 2004; Frid et al. 2005; Scandol et al. 2005).

Measuring or estimating the abundance of pelagic fishes has long been problematic for fisheries scientists. Pelagic fishes are generally fast-swimming and wide-ranging and

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can vary greatly in mass from less than a kilogram (small mackerels and bonitos) up to hundreds of kilograms (tunas and billfishes). This makes them difficult to sample by methods that are often used to estimate fish densities, such as trawling. In trawl catches, fish abundance can be estimated because the area covered by the trawl can be calculated from the spread of the net opening, trawl duration, and trawl speed and by including a catchability coefficient for each species (Blaber et al. 1990; King 1995). However, large pelagic fishes can easily avoid trawl gear as trawls are often towed at low speeds and cover only a relatively small proportion of the water column.

Aerial surveys have been used to estimate abundance of commercially important tunas (Cowling and Polacheck 1995; Lutcavage et al. 1997) because large areas can be surveyed relatively quickly. However, this method is expensive, fish weights or lengths cannot be measured accurately, and species differentiation can be poor (Bell 1976). The accuracy of a survey is also dependent on a number of factors affecting the visibility of fish (e.g., wind and cloud cover) and experience of the observer(s) (Cowling and Polacheck 1995).

The most effective methods for capturing pelagic fishes are gillnets and longlines, which are used by many pelagic fisheries worldwide (Food and Agriculture Organization of the United Nations 2005). Gillnets are effective because they can cover large areas and be selective for particular species by the size and type of mesh used and depth at which they are set. They are a passive fishing method whereby the probability of fish being caught depends on their mobility, body shape, and size. The most critical factor is body girth, as capture generally depends on a fish wedging its head into a mesh to a point past the operculum (Hamely 1975). Unfortunately for scientists, gillnets are not particularly useful for estimating fish abundance in most situations for a variety of reasons, the main reasons being that many fish are able to swim backward on contact with the net or swim slowly enough to be able to detect and avoid the net altogether. Furthermore, many fish species are able to maintain a constant position in the water column, meaning that a fish's probability of encountering a gillnet set nearby may bear no relationship to the net's soak time. Consequently, it is difficult to determine the effective area fished by a gillnet in order to estimate the abundance or biomass of a species in a discrete area.

As an exception, fast-moving oceanic pelagic fishes may be one of the few fish groups for which abundance may be reasonably estimated from gillnet catches. Many pelagic fishes, namely scombrids and istiophorids, are obligate ram ventilators (Brown and Muir 1970). They need to constantly move forward to maintain oxygen supply to the gills to facilitate their high metabolic rates, as well as maintain buoyancy. This is particularly important in species lacking a swim bladder (Korsmeyer and Dewar 2001). Consequently, most pelagic fish have little capability of swimming backwards on contact with a gillnet. The high speed at which they generally encounter a net can result in a high probability of capture given a suitable mesh size (Cameron and Begg 2002).

Therefore, by using information on the sustained swimming speed of a species, it may be feasible to calculate the maximum distance from which a fish can interact with a gillnet set for a given period. This will provide an estimate of the effective fishing area of the net. By incorporating information on the size selectivity of the net to determine the proportion of the population that may not be well represented in the catch, an estimate of abundance is possible.

This paper describes a novel Bayesian modelling approach to estimate the abundance of pelagic fishes in data-limited situations from gillnet catch data combined with elicited information from experts regarding the size structure of the population in the study region and published fish swimming speeds. We developed the model to provide abundance estimates and, subsequently, biomass of pelagic fishes for an ecosystem model of a discrete region (herein referred to as Weipa) of Australia's second most valuable fishery, the Northern Prawn Fishery (NPF). Our only source of information on pelagic fishes was gillnet catch data from fishery-dependent scientific surveys and anecdotal information from expert fish ecologists with knowledge of pelagic fishes in the region. In this paper we provide abundance estimates for four pelagic scombrids (grey mackerel, *Scomberomorus semifasciatus*; Spanish mackerel, *Scomberomorus commerson*; longtail tuna, *Thunnus tonggol*; leaping bonito, *Cybiosarda elegans*) and two istiophorids (Indo-Pacific sailfish, *Istiophorus platypterus*; black marlin, *Makaira indica*) common in the waters of northern Australia. The model will have wider application to various ecosystems and fisheries worldwide.

Materials and methods

Collection of gillnet data

The catch data used in this study were collected by scientific observers in Queensland's N9 offshore shark gillnet fishery along the eastern coast of the Gulf of Carpentaria, near Weipa in northern Australia (Fig. 1). Data were collected between March 2001 and April 2005 by scientific observers from CSIRO Marine and Atmospheric Research and Queensland Department of Primary Industries and Fisheries (QDPI&F) independently monitoring catches in this fishery for different purposes. For example, QDPI&F monitored the catch and bycatch in this fishery, whereas CSIRO collected pelagic fishes for biological and dietary analyses.

In total, 268 sets were monitored whereby observers recorded net length and drop, mesh size and material (in this case, 165 mm monofilament), set type (surface or bottom set), deployment and winching time, total soak time, total number of each species, and the fork length of individual fish. The length of the net used in each set ranged between 300 and 2200 m, with the average net length being approximately 1400 m. Gillnet soak times ranged between 1.3 to 9.7 h, although the average set was about 4.5 h.

We only included 208 sets taken during the night when pelagic fishes do not generally actively feed (Ménard et al. 2000; Griffiths et al. 2007). During this time they are more likely to swim at a more constant speed and their spatial distribution should be less biased by the presence of prey aggregations. To account for possible differences in the susceptibility of each species to capture by the fishing gear because of diel vertical migrations (Brill et al. 1999; Pepperell and Davis 1999; Schaefer and Fuller 2002), we

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Fig. 1. Map of the Weipa study region where gillnet sampling for pelagic fishes took place. Inset map shows the location of the study region (black rectangle) in northern Australia.

only included surface sets in which the net covers approximately the top 10 m of the water column.

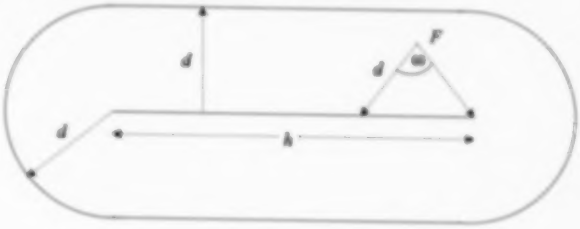
Because regulations in the N9 fishery restrict fishers to using nets with 165 mm mesh, we sought data collected by other methods or gillnet mesh sizes that would allow us to glean more information about the 'true' size structure of the population of each species in the study region. A major data source was catch data collected by CSIRO scientific observers onboard Taiwanese gillnet vessels that operated in Australia's NPF from 1979 to 1986 (Stevens and Davenport 1991). These vessels deployed gillnets with 145–190 mm monofilament mesh of an average length of 16 000 m and depth of 15 m with each set lasting for 6–9 h. We also used data collected from scientific surveys with rod and line (Griffiths et al. 2007). Published catch data from longlines of various lengths and surface-set gillnets of 1200 m in length with monofilament mesh of 100, 150, and 200 mm (Lyle and Timms 1984; Lyle 1987) were also included in the analyses. Despite the total catch of pelagic fish in these studies being generally too low to undertake detailed size-selectivity analyses, they provided valuable data on the size range of the population of each species in the region.

We restricted our analyses to four scombrids (grey mackerel, Spanish mackerel, longtail tuna, leaping bonito) and two istiophorids (Indo-Pacific sailfish and black marlin). We selected these species for several reasons: (*i*) they are common in northern Australia and represent a number of ecological functional groups in the region; (*ii*) they vary significantly in size and body form; and (*iii*) they were caught in sufficient numbers in our samples to allow statistical analyses.

Model building and assumptions

The method makes a number of simple assumptions in a two-stage process of estimating fish abundance: (stage 1) determine the abundance of fish directly from counts of fish from gillnet catches by incorporating gillnet length, net soak time, and fish swimming speed, and then (stage 2) adjust the abundance estimate for particular size classes that are known to be in the sampling region but are underrepresented in the catch because of the size selectivity of the gear.

Fig. 2. A set gillnet and its "domain of potential interaction". Under the assumptions, when the net is set, no fish outside the domain of potential interaction can reach the net in time to be caught. See text for definitions of variables.



Suppose that a gillnet of length h, indicated by a single central horizontal line (Fig. 2), is set for a known period of time. We may assume that the pelagic fishes are (*i*) continuously swimming and that they swim in straight lines within the range of the net (*ii*) at a constant known speed and (*iii*) in a random direction uniformly distributed over the compass directions. We also assume that all fish within the defined size distribution for the region (see Adjusting for size selectivity) are equally available for capture by being distributed within the drop of the net (in this case within 10 m of the surface) and do not undertake diel vertical migrations, as there is no evidence of this occurring in the relatively shallow waters of the Gulf of Carpentaria.

We made additional assumptions that there was no avoidance of the net by fish (because all sets were made at night), and once a fish encountered the net, it was captured. Subsequently, there was assumed to be no "drop-out" of fish from the net, which is largely supported by gillnet drop-out experiments conducted in a pelagic gillnet fishery in northern Australia (Cameron and Begg 2002). Finally, we assumed that gillnet saturation did not occur during any gillnet set. Saturation is the effect of catching so many fish in the net at one time that there is a reduced probability that additional fish may be caught. Because most sets were relatively short compared with the large size of nets used, this was assumed unlikely to have occurred. Underestimates in abundance would be expected if our model was used in situations in which these assumptions are violated.

If d is the maximum distance that a fish can swim while the net is set, then the "domain of potential interaction" consists of a rectangular region with sides parallel to the net at a distance d away from it, together with two semicircular regions at each end of radius d (Fig. 2). Under the assumptions, when the net is set, no fish outside the domain of potential interaction can reach the net in time to be caught.

A fish at some position F within the domain of potential interaction swims in a random direction and may reach any point on a circle of radius d centred on the initial point F. This circle will intersect the net at one or two points, and the angle at F defined by the section of the net within this circle, denoted by ω (Fig. 2), specifies the range of directions that

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the animal may take to reach the net. If we further assume that any fish reaching the net is caught, then the probability that an animal initially located at the point F is caught by the net is

$$(1) \qquad \Pr(\text{capture}|F) = \omega/2\pi$$

We may think of ω as a function of geographical coordinates, $\omega = \omega(x, y)$. If we further assume that fish are randomly distributed within the domain of interaction at the time that the net is set, the average proportion of fish caught within the domain of interaction is then the average of this conditional probability over the region:

$$(2) \qquad p = \frac{\iint_D \omega(x, y)\,dx\,dy}{2\pi(2dh + \pi d^2)}$$

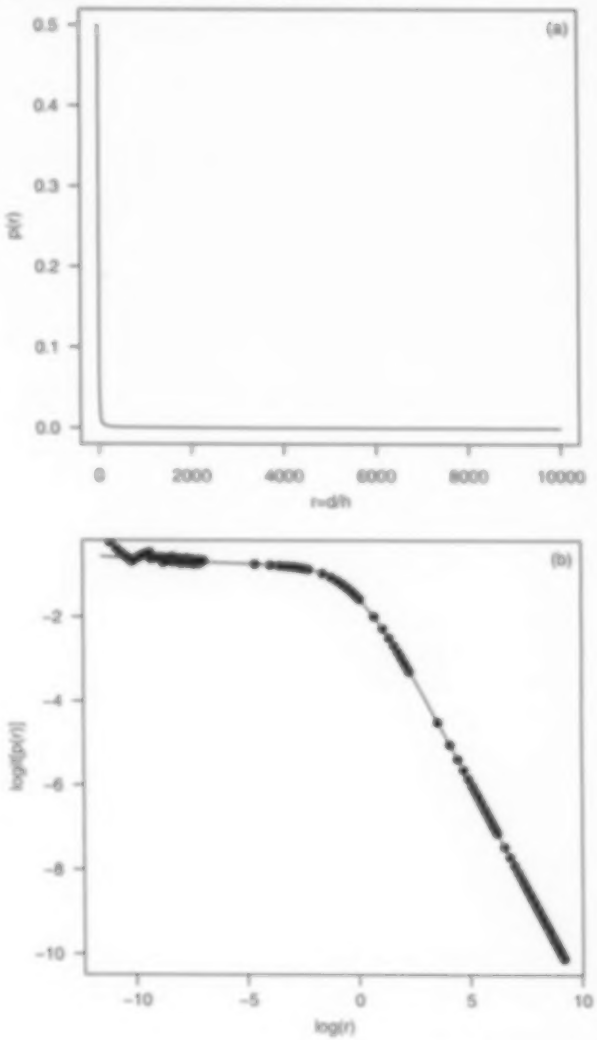
where the integral is over the domain of interaction, say D, with area $2hd + \pi d^2$.

This average proportion, p, will depend on d and h only through the ratio $r = d/h$. To see this, note that the result is clearly invariant with respect to the units in which we measure the lengths involved. Hence if we choose the measurement unit to be the length of the gillnet itself, h becomes unity and the quantity denoted by d becomes d/h. Hence, algebraically the result can only depend on this ratio. It is not possible to evaluate this integral in closed form, but it is possible to get a good approximation of it by numerical quadrature (Fig. 3). As d/h approaches infinity, the probability of encountering the net tends to zero, while it is also clear that p lies between 0 and 0.5 (Fig. 3*a*). Higher probabilities of interaction with the net occur near the central point of the gillnet, whereas lighter regions indicate that the chance of a fish being captured by the gillnet is reasonable low (Fig. 4).

An alternative approach to evaluating $p(r)$ is through a piecewise cubic spline approximation developed to explain the relationship between logit(p) and log(r) (Fig. 3*b*). Here, the points are the result of numerical quadrature, and the solid line represents the piecewise cubic spline approximation. We used the "splines" package in R (Ihaka and Gentleman 1996) to construct this relationship using information for four main parameters (Table 1). Each row represents a cubic function constructed over an interval $a:b$ (on the log scale), centred around the lower boundary of that interval. For example, for the interval $\log(r) \le -10$, we use the constant –0.7626896 to approximate logit(p). If $-10 < \log(r) \le -7.78$, we use the following approximation:

$$(3) \qquad \text{logit}(p) = -0.7626896 + 0.007790967(\log(r) + 10) - 0.001570167(\log(r) + 10)^3$$

Fig. 3. Plots showing (*a*) the average probability of capture in the domain of potential interaction and (*b*) the cubic spline approximation of the transformed probability.



Statistical models and estimation

Let γ be the average relative abundance, which represents the average number of fish per unit area. If Y is the number caught in the gillnet, then the mean of Y is

$$(4) \qquad \mu = E(Y) = \gamma[p(d/h)(2hd + \pi d^2)] = \gamma\left\{\frac{1}{2\pi}\iint_D \Phi(x, y)\,dx\,dy\right\} = \gamma A(h, d)$$

where we may think of $A(h,d)$ as the "equivalent area" of the domain of potential interaction, i.e., the area of a region in which the mean number of fish equals the average number caught in the gillnet.

The distribution of Y is clearly discrete, and for fish that occur only sparsely within the domain of interaction, a natural model is to assume that Y has a Poisson distribution (McCullagh and Nelder 1989). This will be a credible model if the fish occur at random within the domain of potential interaction, but if there are large schools of fish captured by the gillnet, then the negative binomial distribution may be more appropriate (Lawless 1987; McCullagh and Nelder 1989). If there are very few captures resulting in a large number of zeros, a zero-inflated mixture model such as a zero-inflated Poisson (ZIP) or zero-inflated negative binomial (ZInb) model may be considered (Lambert 1992; Welsh et al. 1996; Kuhnert et al. 2005). These models have been

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Fig. 4. Image plot of probabilities in the domain of potential interaction. Darker shading indicates higher probabilities of interaction towards the gillnet.

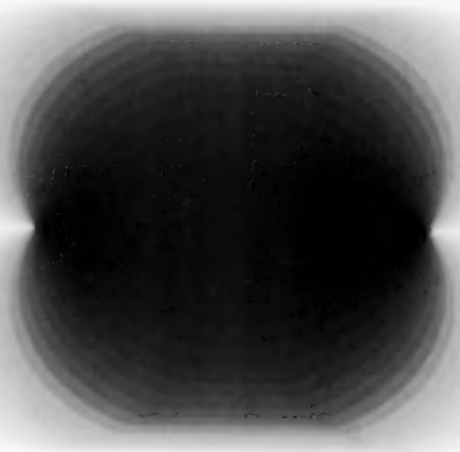

Table 1. Coefficients used in the piecewise cubic spline approximation for specified intervals.

Interval	Constant	Linear	Quadratic	Cubic
$\text{logit}(r) \le -10$	−0.762 689 6	0	0	0
$-10 < \text{logit}(r) \le -7.78$	−0.762 689 6	0.007 790 967	0	−0.001 570 167
$-7.78 < \text{logit}(r) \le -5.56$	−0.762 607 3	−0.015 470 773	−0.010 467 783	0.004 025 204
$-5.56 < \text{logit}(r) \le -3.33$	−0.804 507 2	−0.002 361 607	0.016 366 908	−0.009 485 520
$-3.33 < \text{logit}(r) \le -1.11$	−0.833 024 5	−0.070 146 021	−0.046 869 894	−0.011 011 937
$-1.11 < \text{logit}(r) \le 1.11$	−1.341 205 1	−0.441 596 465	−0.120 282 805	0.007 879 952
$1.11 < \text{logit}(r) \le 3.33$	−2.830 045 7	−0.859 446 684	−0.067 749 794	0.011 076 719
$3.33 < \text{logit}(r) \le 5.56$	−4.952 938 8	−0.996 457 336	0.006 095 00	−0.001 245 409
$5.56 < \text{logit}(r) \le 7.78$	−7.150 856 7	−0.987 818 946	−0.002 207 725	−0.001 408 638
$7.78 < \text{logit}(r) \le 10$	−0.372 370 6	−1.018 499 767	−0.011 598 645	0.001 739 797
$\text{logit}(r) > 10$	−11.673 888	−1.044 274 533	0	0

applied to various applications in the ecology literature and are most useful when information about the source of the zero inflation is available.

We consider a Bayesian hierarchical model that incorporates the prior information for swimming speeds and assumes a negative binomial distribution for the counts of each species of fish. We explored the Poisson, ZIP, and ZInb models for this problem and found that the best model by far was the negative binomial model. This model has the capacity to take into account large counts due to schooling fish, as well as zero inflation, which was evident in many of the datasets. Furthermore, the negative binomial model performed the best in terms of the deviance information criterion (DIC) (Spiegelhalter et al. 2002). Results in the following sections will therefore be based on this model.

The model can be formulated generally as shown in eq. 5. Here, the mean, μ, is modelled on the log scale and represents the probability of fish caught in set i residing in the domain of potential interaction as determined by the cubic spline (CS) approximation; h_i represents the net length; and d_i represents the maximum distance that fish i can swim to the net, which is comprised of the duration, t_i, and swimming speed, s_i. The negative binomial parameter is represented by θ and is defined through $\text{Var}(Y) = \mu + \mu^2/\theta$. Note that we define area in square kilometres, so the estimate of abundance is number of fish per square kilometre (fish·km^{-2}).

$$\Pr(Y_i = y_i) = \frac{\Gamma(\theta + y_i)}{\Gamma(\theta) y_i!} \frac{\theta^{\theta} \mu_i^{y_i}}{(\theta + \mu_i)^{\theta + y_i}} \quad (5)$$

where

$$\log(\mu_i) = \log(\gamma) + \log[A(h_i, d_i)]$$

and

$$\log[A(h_i, d_i)] = \log[p(d_i/h_i)] + \log(\text{Area}_i)$$

$$\log(\text{Area}_i) = \log(d_i) + \log(2h_i + \pi d_i) - \log(10^6)$$

$$d_i = t_i s$$

$$\text{logit}[p(d_i/h_i)] = \text{CS}(d_i/h_i)$$

and $\lambda = \gamma s$ and s have independent priors

$$\log(\lambda) \sim N(0, 10)$$

$$(s - 23) \sim \text{Ga}(\alpha, \beta)$$

We originally considered a noninformative prior for the relative abundance parameter γ described earlier. However,

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Table 2. Summary statistics and parameters used to define the prior swimming speeds (m·min^{-1}) for two pelagic fish groups: scombrids and istiophorids.

	Swimming speed		Parameters for prior	
Fish groups	Mean	Standard deviation	α	β
Scombrids	15.50	10.66	2.1062	0.1363
Istiophorids	25.96	12.06	5.0136	0.1918

as γ and the parameter for swimming speed, s, are related (i.e., to estimate abundance, we need to know something about the speed at which the fish swims), we placed a prior on their product, $\lambda = \gamma s$. This specification recognises that the priors placed on λ and s will be independent. We consider this more realistic than assuming, for example, that γ and s have independent priors, and this is somewhat reflected by the fact that the convergence of the computational algorithm is improved. The prior chosen for $\log(\lambda)$ was a normal distribution with a mean of zero and variance 10, i.e., with precision 0.1 in the measurement units chosen. This represents a fairly noninformative prior, as is appropriate. The term "precision" refers to the inverse of the variance and is typically represented by the parameter τ. The estimate of abundance, γ, can then be found through the ratio of the posterior distributions of λ and the swimming speed of the fish.

We place a fairly noninformative gamma prior on the overdispersion parameter, θ, selecting parameters for this distribution that were sensible for the application at hand.

Because of the computational nature of the problem, in particular the evaluation of the spline approximation, we coded up the problem in C using the Metropolis–Hastings algorithm (Gilks et al. 1996; Gelman et al. 2004) to generate samples from the respective posterior distributions. In addition, we appropriately scaled the input variables to encourage adequate mixing of the Markov chains. Estimates were obtained from 10 000 iterations after an initial burn-in of 10 000 iterations. Convergence was assessed using the CODA package in R (Best et al. 1995).

A prior for random swimming speeds

The assumption of a constant swimming speed for all animals is unrealistic, but reasonable in this modelling context. We used published swimming speeds for the same or similar-sized scombrid and istiophorid species examined in the present study, including yellowfin tuna (*Thunnus albacares*) (Sambilay 1990; Block et al. 1997), bigeye tuna (*Thunnus obesus*) (Sambilay 1990; Schaefer and Fuller 2002), southern bluefin tuna (*Thunnus maccoyii*) (Davis and Stanley 2002), albacore (Dotson 1976), Pacific bonito (*Sarda chiliensis*) (Dowis et al. 2003), skipjack (*Katsuwonus pelamis*) (Sambilay 1990), black marlin (*Makaira indica*) (Pepperell and Davis 1999), and blue marlin (*Malzaira nigricans*) (Holland et al. 1990; Block et al. 1992; Graves et al. 2002). This information was used to develop two informative priors for two groups: scombrids (tunas and mackerels) and billfishes (sailfish and black marlin).

To reflect uncertainty in the swimming speed, we considered an informative prior of the form

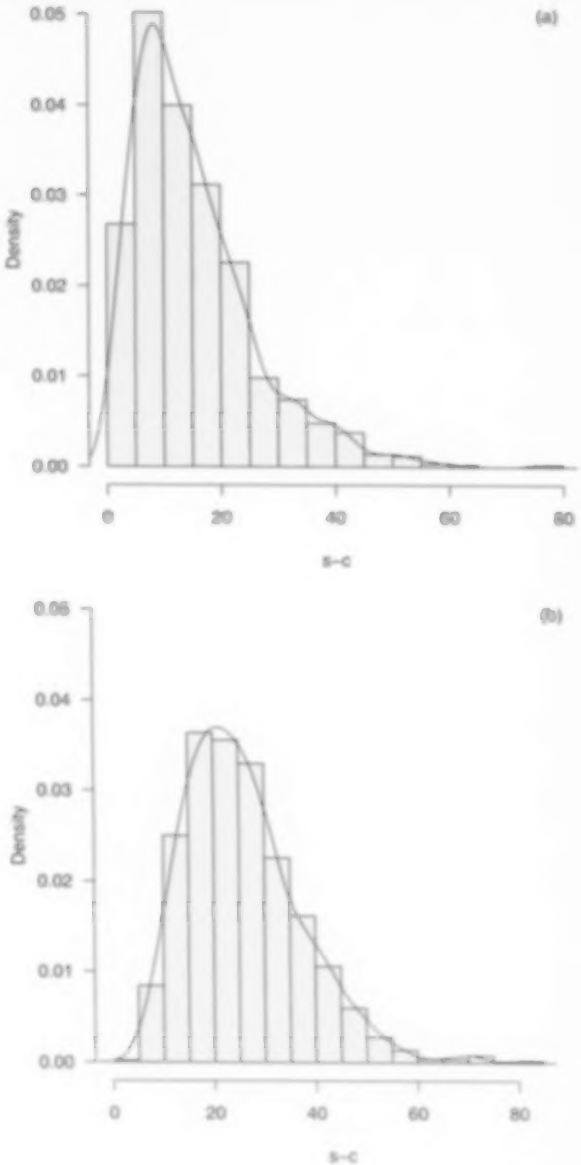

Fig. 5. Informative prior distribution for the shifted swimming speed, $s - c$, for (*a*) scombrids (tunas and mackerels) and (*b*) istiophorids (black marlin and sailfish). Speeds are recorded in metres per minute.

$$(s - c) \sim \mathrm{Ga}(\alpha, \beta)$$

where c is a constant that shifts the distribution of s to the lowest possible swimming speed for scombrids (c = 23 m·min^{-1}), and α and β represent, respectively, the shape and scale parameters for the gamma distribution. The parameters α and β were determined from the published swimming speeds and were then used to construct prior distributions for the two pelagic fish groups (Table 2; Fig. 5). The average

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sustained swimming speeds of fish were 15.50 m·min^{-1} (scombrids) and 25.96 m·min^{-1} (istiophorids).

Adjusting for size selectivity

The methodology for estimating the abundance of fish to this point does not take into account the size selectivity of the 165 mm mesh gillnets used the N9 fishery. An estimate of size selectivity was incorporated into the existing method to account for size classes that were known, or suspected, to be available in the area but were not well represented in the catch because of the gillnet's size selectivity.

If the size selectivity, p_c, was known for a given net size, then the abundance estimates in the model could be adjusted for size selection by

$$(6) \qquad \Pr(Y_i = y_i) = f(y_i; \psi_i = p_c\mu_i, \theta)$$

where p_c is the probability of capture, ψ_i is the observed mean density of the ith shot, and μ_i is the true mean density for the ith shot.

In the above expression, p_c can represent a uniform prior of probabilities between an elicited lower and upper interval having support between 0 and 1. Alternatively, a mathematical expression can be found for p_c with additional input from an expert regarding the length distribution of the 'true' population, and a single probability can be input into the model. Expert opinion is required in this instance as there is little quantitative catch and size distribution data for most pelagic fish species in northern Australia. Furthermore, experts with experience fishing for pelagic species in the region have reliable knowledge of expected size distributions.

Consider the population abundance of lengths, $\phi(l)$ (measured as fork length), for a fish with an average length $\bar{l}$. We also consider the selectivity of a fish given its length, $\Pr(c|l)$. An expression for the abundance of observed lengths of a pelagic species given that it is captured in the gillnet can be written as

$$(7) \qquad f(l|c) = \frac{\Pr(c|l)\phi(l)}{\int_0^\infty \Pr(c|l)\phi(l)dl} = \frac{\Pr(c|l)\phi(l)}{p_c}$$

The expression for p_c in eq. 7 can be thought of as the area under the population abundance density, $\phi(l)$, weighted by the size selectivity. So if $\Pr(c|l) = 1$, then all individuals having a specific length in the population are captured. However, we know that this will not be the case given that the size of the mesh influences the size and, therefore, the number of fish caught. Therefore, if $\Pr(c|l) < 1$, only a proportion, $\Pr(c|l)$, of the population is captured. Rearranging eq. 7 to provide an expression for size selectivity is

$$(8) \qquad \Pr(c|l) = p_c \frac{f(l|c)}{\phi(l)}$$

From the above expression, we know that $\Pr(c|l)$ is equal to one when the ratio of the observed lengths density given capture and the population abundance density is at its maximum. If we assume that $f(l|c)$ and $\phi(l)$ are both normal densities (based on empirical data for pelagic species in the region), we can write down the following expression for this ratio, where μ_f and σ_f^2 represent the mean and variance, respectively, for the density of lengths given capture, and μ_ϕ and σ_ϕ^2 represent, respectively, the mean and variance for the population density of lengths.

$$(9) \qquad \text{Ratio} = \frac{f(l|c)}{\phi(l)} = \frac{\frac{1}{\sqrt{2\pi}\sigma_f}\exp(-0.5(l-\mu_f)^2/\sigma_f^2)}{\frac{1}{\sqrt{2\pi}\sigma_\phi}\exp(-0.5(l-\mu_\phi)^2/\sigma_\phi^2)}$$

Taking logs of this expression gives

$$(10) \qquad -\log(\sigma_f) - \frac{0.5(l-\mu_f)^2}{\sigma_f^2} + \log(\sigma_\phi) + \frac{0.5(l-\mu_\phi)^2}{\sigma_\phi^2}$$

and differentiating with respect to l and setting the expression to zero to solve for $\tilde{l}$ provides an expression for the estimated fork length at the maximum.

$$(11) \qquad \tilde{l}\left(\frac{1}{\sigma_\phi^2} - \frac{1}{\sigma_f^2}\right) + \frac{\mu_f}{\sigma_f^2} - \frac{\mu_\phi}{\sigma_\phi^2} = 0$$

$$\tilde{l} = \frac{\mu_\phi\sigma_f^2 - \mu_f\sigma_\phi^2}{\sigma_f^2 - \sigma_\phi^2}$$

Substituting $\tilde{l}$ into the expression for the ratio and rearranging gives

$$(12) \qquad \text{Ratio} = \frac{f(\tilde{l}|c)}{\phi(\tilde{l})} \text{ and } p_c = 1/\text{Ratio}$$

Equation 12 is an expression for size selectivity, p_c, in which $f(\tilde{l}|c)$ is based on our best guess from expert information, conditioned on some historical data. However, the population abundance $\phi(\tilde{l})$ is largely unknown, and to evaluate this expression, we need to elicit information about this parameter for the species of interest.

Elicitation of $\phi(l)$

The elicitation of information regarding the length distributions of the "true" population for each pelagic species was a three-stage process.

First, relevant data were extracted for the distribution of lengths for each pelagic species to develop an appropriate prior distribution for $\phi(l)$. This distribution also incorporated expert information about the region and likely catches for each pelagic species. To complete this first stage of the elicitation process, we used catch data from a Taiwanese gillnet fishery, which operated in Australia's NPF from 1979 to 1986, from scientific sampling using longlines, gillnets, and rod and line to provide a baseline from which a population abundance could be extracted. We sought input from a fish biologist with knowledge of the pelagic species and the fishery to determine the shape and structure of this density, which in this case was defined to be a normal distribution.

The second stage involved building a relevant distribution of lengths for the observed catches in the fishery, $f(l|c)$. However, for some species for which the data were scarce, we again relied on expert opinion to provide information

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Fig. 6. Prior distributions for the population fork length (solid line), abundance corresponding to the portion of the population that is missed from gillnet fishing, f(MISS) (dotted line), and observed fork length distribution (broken line) curve in the N9 fishery for (*a*) grey mackerel (*Scomberomorus semifasciatus*), (*b*) Spanish mackerel (*S. commerson*), (*c*) longtail tuna (*Thunnus tonggol*), (*d*) leaping bonito (*Cybiosarda elegans*), (*e*) black marlin (*Makaira indica*), and (*f*) Indo-Pacific sailfish (*Istiophorus platypterus*). Components of the population that are missed by the N9 fishery are represented by the dotted line. The selectivity function is shown beneath each plot and represents the probability of capture, Pr($c|l$). Size distribution data used to define the prior distributions are shown for the N9 fishery (darker shading) and the overall population comprised of various sampling methods (lighter shading).

about the shape, centre, and extreme values of this distribution.

The final stage of the elicitation process involved using a graphical aid to visualise the elicited distributions and confirm their validity through the construction of the selectivity function using the expression shown in eq. 8. We found this graphical aid useful for confirming the expert's judgement in situations where little data had been collected for a particular species.

The results of the elicitation process for the six pelagic species investigated shows the distribution elicited for that population ($\phi(l)$; Fig. 6, solid black line), the distribution elicited for the observed lengths in the fishery ($f(l|c)$; Fig. 6, broken line), and the abundance corresponding to the portion of the population that is missed from gillnet fishing (f(MISS); Fig. 6, dotted line). The latter abundance was derived from the expression

$$f(\text{MISS}) = \frac{(1 - \Pr(c|l))\phi(l)}{1 - p_c} \quad (13)$$

Length frequency data used to derive the "true" population distribution (Fig. 6, lighter shaded bars) and the fishery are also shown, and the plot below each figure shows the size selectivity function, Pr($c|l$).

For the majority of species, the observed length distributions in the fishery capture the majority of the population reasonable well, although because of the morphology of each species, some parts of the size distribution are underrepresented in the catch. For example, grey mackerel and black marlin catches match the population quite closely, with the selectivity function indicating that only a small proportion of the larger grey mackerel (>85 cm) and black marlin (>200 cm) are underrepresented in the N9 catch. Sailfish, Spanish mackerel, and leaping bonito all show a bell-shaped selectivity function, indicating that the highest proportion of fish caught is mid-ranged in terms of size.

In determining the population length distribution for each species, catches from all data sources were used. These gave a reasonable baseline from which to elicit the distribution for all fish, with the exception of longtail tuna. We found that the size distribution of longtail tuna from the Taiwanese gillnet catches (Stevens and Davenport 1991) was comprised of much smaller fish than what was observed in the N9 fishery, resulting in a probability of capture of approximately 0.004. It has been hypothesised that this species utilises areas in northwestern Australia as a nursery, which is where the Taiwanese operation primarily took place. The species then appears to undertake an ontogenetic migration to the eastern Gulf of Carpentaria (Serventy 1956), where typically larger individuals become available to the N9 fishery.

To validate this theory, we extracted additional information from two independent surveys conducted in the eastern Gulf of Carpentaria and compared this information with data collected from the Taiwanese and the N9 fisheries. We found that the independent surveys were similar to the N9 catches, and therefore, we were able to derive a more plausible population distribution using this data in conjunction with expert opinion about the fishery and longtail tuna. The resulting distributions for $f(l|c)$ and $\phi(l)$ from this elicitation exercise (Fig. 6c, broken and solid lines, respectively) show a smaller proportion of the juveniles being underrepresented. This compared favourably with previous calculations (dotted line) and resulted in a probability of capture of 0.27.

Validation of model abundance estimates

The majority of species used in this study have little or no commercial value. Consequently, it is difficult to validate the abundance estimates for each species from our model with an independent data source. Grey and Spanish mackerel are highly valuable commercial species in the region. Detailed catch data for three types of fisheries (commercial, net and line, and sportfish) exists for the Albatross Bay region (Fig. 1) and can be used to compare with our model estimates.

We converted our abundance estimates for grey and Spanish mackerel to biomass (kg·km^{-2}) because our model deals with fish counts and the commercial catch only reports total biomass for the region. Because we knew the size distribution of the N9 catch, we used a weighted average of fish mass in each size class from the length–weight relationship of Cameron and Begg (2002) multiplied by the abundance of fish calculated by the model. We then scaled up this figure to a total biomass for the defined Albatross Bay N9 fishery region (5 788 km^2) (see Okey 2006). This was our only means to validate our model results. We made the assumption that our model needed to at least exceed the combined commercial and sportfish catch in the region to be representative of the "true" population abundance.

The average annual catch of grey and Spanish mackerel combined for all commercial and sportfish fisheries in the region between 2001 and 2004 when our sampling was conducted was 37.7 and 20.3 tonnes (t)·year^{-1}, respectively. These catches needed to be at least exceeded for our model estimates to be reasonable.

Results

Results from fitting the gillnet model to eight pelagic species are shown (Tables 3 and 4), which include the posterior mean, standard deviation, and 95% confidence interval (CI) for the swimming speed (s) of each fish and the overdispersion parameter (θ) resulting from the negative binomial model. It is clear from this table that the swimming speed posterior mean summaries reflect the informative prior chosen for each species. Overdispersion was evident in all

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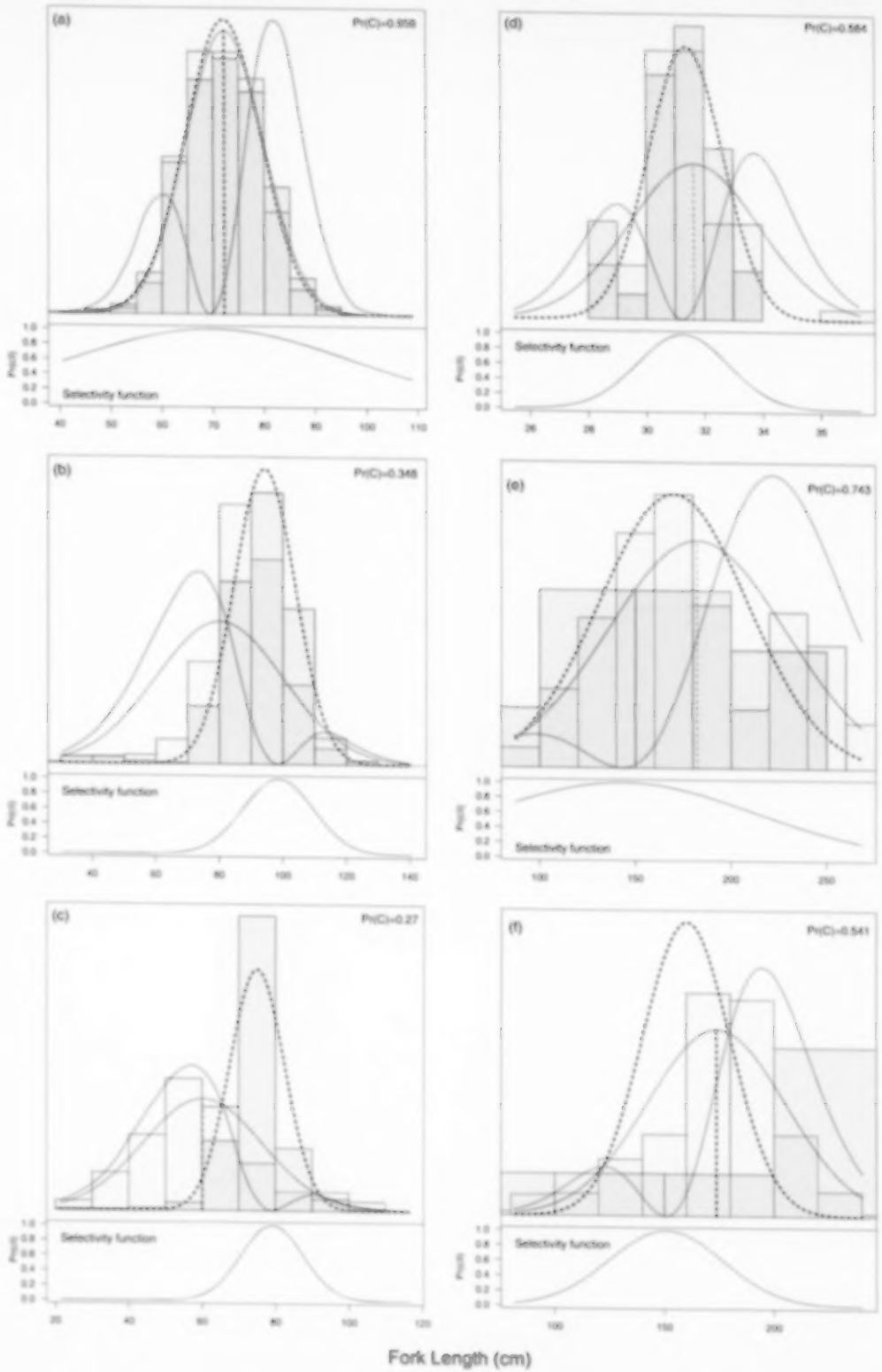

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Table 3. Results from fitting the negative binomial model to the gillnet catch data of six pelagic fish species. Posterior mean estimates, standard deviations (SD), and 95% credible intervals (CI) are shown for the swimming speed (s) and overdispersion parameter (θ).

	Swimming speed (s)			Overdispersion (θ)		
Species	Estimate	SD	95% CI	Estimate	SD	95% CI
Black marlin	48.870	11.337	(31.79, 75.32)	3.8100	6.046	(0.03, 20.27)
Sailfish	48.622	11.329	(31.66, 75.78)	3.7557	5.902	(0.03, 20.27)
Longtail tuna	39.101	11.054	(25.09, 67.15)	0.2779	0.035	(0.21, 0.35)
Grey mackerel	39.026	10.748	(25.16, 65.36)	0.2740	0.028	(0.22, 0.33)
Spanish mackerel	38.567	10.769	(25.04, 65.86)	0.4103	0.056	(0.32, 0.53)
Leaping bonito	37.996	10.229	(25.15, 63.58)	0.0590	0.024	(0.03, 0.12)

Table 4. Results from fitting the negative binomial model to the gillnet catch data of six pelagic fish species. Posterior mean estimates, standard deviations (SD), and 95% credible intervals (CI) are shown for the density (γ) and adjusted density (γ^*), which takes into account size selection.

	Density (γ)				Adjusted density (γ^*)		
Species	Estimate	SD	95% CI	p_z	Estimate	SD	95% CI
Grey mackerel	3.9754	1.087	(2.090, 6.208)	**0.9582**	4.1737	1.167	(2.173, 6.641)
Longtail tuna	0.4915	0.139	(0.257, 0.780)	**0.2705**	1.8099	0.499	(0.965, 2.874)
Spanish mackerel	0.3986	0.106	(0.206, 0.616)	**0.6388**	1.1455	0.304	(0.608, 1.758)
Leaping bonito	0.0244	0.012	(0.009, 0.053)	**0.5643**	0.0438	0.021	(0.017, 0.096)
Black marlin	0.0032	0.002	(0.001, 0.007)	**0.7434**	0.0042	0.002	(0.001, 0.009)
Sailfish	0.0027	0.001	(0.001,0.006)	**0.5408**	0.0050	0.003	(0.002, 0.012)

Note: Probability of capture (p_z) is in bold.

eight models as it took into account large counts due to schooling fish, particularly for grey mackerel, as well as zero counts for species such as black marlin and sailfish.

Abundance estimates for the six species before and after adjusting for size selection are shown (Table 4). The posterior estimates for swimming speed and overdispersion did not change once the adjustment for size selection was incorporated into the model and are therefore not replicated in Table 4.

Abundance estimates did not change substantially for most pelagic fish investigated after being corrected for size selectivity, indicating that the size distribution of fish in the N9 fishery closely reflected that of the population (Fig. 6). An exception was longtail tuna, which increased from 0.49 to 1.81 fish·km^{-2} after adjusting for size selectivity. This was primarily due to small size classes in the population (40–70 cm) not being well represented in the N9 catch (Fig. 6*a*).

After adjusting for size selectivity, the highest abundance estimate was obtained for grey mackerel (4.17 fish·km^{-2}, 95% CI = 2.17, 6.64). Interestingly, the abundance of the closely related Spanish mackerel was considerably lower (1.15 fish·km^{-2}, 95% CI = 0.61, 1.76). Relatively low abundance estimates were obtained for the smallest scombrid, leaping bonito (0.04 fish·km^{-2}, 95% CI = 0.12, 0.10). The lowest abundance estimates were obtained for the two istiophorids, marlin (0.004 fish·km^{-2}, 95% CI = 0.001, 0.009) and sailfish (0.005 fish·km^{-2}, 95% CI = 0.002, 0.012).

The only two species of commercial importance in our study region, grey and Spanish mackerel, were used to validate the results from our model by making comparisons with the average annual combined catch from commercial and sportfish fisheries in the region for the years when our gillnet samples were taken (2001–2004). Our model estimates that the annual average standing biomass (±SE) of grey and Spanish mackerel was 78.47 t (0.315) and 35.67 t (0.16), whereas the average annual reported catch was 37.68 and 20.30 t, respectively.

Discussion

Estimating the abundance or biomass of pelagic fishes captured by passive fishing gear, e.g., gillnets, is a difficult and complex proposition that only a few studies have attempted to address (Rudstam et al. 1984; Hansson and Rudstam 1995; Porch et al. 2002). This problem is exacerbated for species of little economic importance because few data are generally available to populate data-intensive models (Rudstam et al. 1984). In northern Australia, many low-value pelagic fishes (e.g., scombrids and istiophorids) occupy high trophic levels and play an important role in structuring tropical ecosystems (Ménard et al. 2000; Griffiths et al. 2007). Knowledge of these less economically important species is likely to become increasingly vital to populate ecosystem models (e.g., Ecopath) that can determine the ecological effects of fishing and facilitate the emerging regime of ecosystem-based fisheries management for many of the world's fisheries (Pauly et al. 2000; Plaganyi and Butterworth 2004). Our Bayesian modelling approach addresses this need by providing a useful means to estimate pelagic fish abundance in data-limited situations by having the capacity to utilise both qualitative expert knowledge and quantitative catch data.

We recognise that our model makes a number of assumptions that may not be entirely realistic. For example, we assume that fish swim in straight lines and in random directions. This is unlikely to be the case as their swimming

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behaviour and probability of capture in a gillnet is likely to be influenced by a range of oceanographic features (Royer et al. 2004; Schick et al. 2004) and other factors, including the proximity of fish to reefs, seamounts, landmasses, and fish aggregating devices (Klimley et al. 2003; Musyl et al. 2003; Ohta and Kakuma 2005). Recent studies using electronic tags are only beginning to reveal the behaviour of some economically important species (Holland et al. 1990; Schaefer and Fuller 2002; Domeier and Dewar 2003). As a result, we feel there are currently too few data on pelagic fish movements in the neritic regime of the Gulf of Carpentaria to warrant inclusion in our model. Nonetheless, we demonstrated that our model using these simple assumptions produced results similar to those of a more sophisticated "random walk" model that incorporated random directional changes in a fish's swimming trajectory (Appendix A).

Perhaps the most influential assumption of our model is that the information on the population size structure for each species elicited from expert opinion is representative of the real size structure. One may think of validating the priors chosen through a sensitivity analysis, a standard mechanism for assessing the plausibility of assumptions made in a model. In this context, this type of approach is neither appropriate nor sensible as the priors are highly informative and important for adjusting the abundance estimates for size selection. As an alternative, we compared the elicited information with quantitative catch data from a number of different sampling methods. This allowed us to verify the quality of anecdotal information from our consulted experts for each species. Of course, data are not always available to achieve this. In circumstances in which species-specific information on the size distribution of the population is unavailable, we believe that our model is still useful when the size selectivity function is excluded. Our results show that for some species this generally results in a conservative abundance estimate of about half that of the estimate when a size-selectivity function is included.

Nonetheless, our model produced ecologically sensible results. We converted our abundance estimates for Spanish mackerel (3.50 kg·km^{-2}; assuming a mean weight of 5.64 kg) and longtail tuna (12.07 kg·km^{-2}; mean weight 6.67 kg) to biomass. Our estimates fell within the range of biomass estimates made for ecologically equivalent species of commercial importance in the tropical eastern and western regions of the Pacific Ocean derived from stock assessment (Cox et al. 2002*a*) or ecosystem models (Godinot and Allain 2003; Olson and Watters 2003). The biomass estimates of wahoo (2.73 kg·km^{-2}), yellowfin tuna (1.3–24.2 kg·km^{-2}), and bigeye tuna (3.5–18.0 kg·km^{-2}) were very similar. Furthermore, the biomass estimates from our model for large species for which we had very little catch data, black marlin (0.13 kg·km^{-2}; mean weight 30 kg) and sailfish (0.10 kg·km^{-2}; mean weight 20 kg), were also very similar to what has been recorded for marlins (0.15–0.57 kg·km^{-2}), swordfish (0.03–0.1 kg·km^{-2}), and sailfish (0.05–0.13 kg·km^{-2}).

Quantitative validation of our model results is extremely difficult given the low commercial importance of the majority of species we examined. In fact, validation of abundance estimates from passive fishing gears for species of high commercial importance has been unsuccessful because of different biases and levels of accuracy of the methods used for validation, e.g., hydroacoustics (Hansson and Rudstam 1995). However, we provided a measure of validation by comparing our biomass-converted model estimates of the two commercially important species with commercial and sportfish catch data. These catch data were independent and were collected concurrently to our study.

Our biomass estimates for both grey and Spanish mackerel in the Weipa region appear reasonable given that the commercial catch comprises about 48% and 56%, respectively, of the estimated population biomass from our model. This is an interesting result considering the probability of capture is substantially higher for grey mackerel ($Pr(c) = 0.96$) than for Spanish mackerel ($Pr(c) = 0.348$). Given the high probability of capture for grey mackerel, it may be expected that the commercial catch would more closely resemble our model estimate. However, the N9 fishery primarily targets sharks, and only targets grey mackerel for a few months of the year. Thus, the population is probably not fully exploited.

In spite of our simple model assumptions, this method of validation of our results indicates that our model is sufficiently robust to provide first-order estimates of pelagic fish abundance (see Appendix A). There is also potential for the model to be modified to become increasingly sophisticated depending on the data available for particular species in other regions. In particular, it has been widely shown that diel vertical migration to surface waters at night is common among many tropical pelagic fishes, including bigeye tuna (Schaefer and Fuller 2002), yellowfin tuna (Brill et al. 1999), blue marlin (Holland et al. 1990), black marlin (Pepperell and Davis 1999), and striped marlin (Domeier and Dewar 2003). This would result in fish being less susceptible to capture by surface set gillnets during the day, leading to underestimates of abundance using our model if catch data were only available from daytime sets.

We did not incorporate a diel vertical migration function in our model for a number of reasons. First, there are no available data on the diel movements of pelagic fishes in the Gulf of Carpentaria. However, Pepperell and Davis (1999) studied the diel vertical migrations of black marlin off the nearby Great Barrier Reef in eastern Australia. They showed that fish regularly dived deeper than 60 m when in water depths of about 200 m but exhibited no significant diel vertical movement in depths of less than 100 m. We presumed that the diel vertical movement of fish in our Weipa study region was probably minimal, as the gillnet sets took place in depths of 9–32 m. Therefore, their movements are probably not significant enough to exclude fish from the path of the 10 m drop of the gillnet.

Second, to minimise the number of assumptions in the model, we only included sets taken during the night, because catches of fish in passive gears can be affected by the net's visibility to fish (Cyrus and Blaber 1992; Griffiths 2001). Furthermore, scombrids and istiophorids are generally high-pursuit, visual predators that mainly feed during the daytime (Ménard et al. 2000; Itoh et al. 2003; Griffiths et al. 2007). Consequently, their horizontal and vertical distribution and swimming speed may be highly influenced by the distribution, movements, and behaviour of their small schooling fish prey. By limiting our data to night samples when these fish

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do not actively feed, the potential variability in catches and swimming speed owing to feeding behaviour may be greatly reduced.

Considering the increasing worldwide interest in ecosystem approaches to fisheries management, estimating the abundance or biomass of low-value, but ecologically important, pelagic species is likely to become increasingly important in future. Most ecosystem models developed to investigate the effects of fishing on ecosystems have generally only utilised commercial catch data for individual pelagic fish species. These data can be used to obtain reasonable biomass estimates using stock assessment, which can then be incorporated in ecosystem models (Cox et al. 2002*a*, 2002*b*). However, some studies estimated biomass of a species by simply dividing the biomass of the commercial catch from the area of interest by the annual fishing mortality rate (F) (e.g., Kitchell et al. 2002). This method would only be appropriate if the annual total mortality rate (Z) is equal to 1, assuming that the remaining population is subjected only to natural mortality (M), given $Z = F + M$. Our model clearly indicates that for the two species for which we had commercial catch data, such approaches would only account for between 48% and 56% of the predicted biomass of these species in the Weipa study region. Therefore, the validity of models based on commercial catch data alone may be compromised by underestimates of this magnitude because pelagic fishes occupy high trophic levels. This would cause an imbalance of energy throughout the modelled system owing to an underestimate of predation pressure on lower trophic levels and an overestimate of predation from other higher trophic level predators (e.g., sharks). In such situations where time or data may be too limited to undertake comprehensive stock assessments to obtain biomass estimates for key pelagic species for ecosystem models, we feel our model provides a cost-effective alternative.

Owing to the great difficulty in quantifying fish behaviour across a variety of spatial and temporal scales, we acknowledge that our model is only an approximation. However, our results indicate that it does produce biologically consistent results. The model we describe provides a useful method for estimating pelagic fish abundance from passive fishing gears in data-limited situations and may be applicable to other animals that move constantly during a discrete sampling period.

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References

Bell, G.R. 1976. Aerial spotting for pelagic fishes. Occ. Publ. Fish. Res. Div. Minist. Agric. Fish. (NZ) No. 11.

Best, N.G., Cowles, M.K., and Vines, S.K. 1995. CODA: Convergence Diagnostics and Output Analysis software for Gibbs sampling output. Version 0.3. MRC Biostatistics Unit, Cambridge, UK.

Blaber, S.J.M., Brewer, D.T., Salini, J.P., and Kerr, J. 1990. Biomass, catch rates and abundances of demersal fishes, particularly predators of prawns, in a tropical bay in the Gulf of Carpentaria, Australia. Mar. Biol. **107**: 397–408.

Block, B.A., Booth, D., and Carey, F.G. 1992. Direct measurement of swimming speeds and depth of blue marlin. J. Exp. Biol. **166**: 267–284.

Block, B.A., Keen, J.E., Castillo, B., Dewar, H., Freund, E.V., Marcinek, D.J., Brill, R.W., and Farwell, C. 1997. Environmental preferences of yellowfin tuna (*Thunnus albacares*) at the northern extent of its range. Mar. Biol. **130**: 119–132.

Brill, R.W., Block, B.A., Boggs, C.H., Bigelow, K.A., Freund, E.V., and Marcinek, D.J. 1999. Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes. Mar. Biol. **133**: 395–408.

Brown, C.E., and Muir, B.S. 1970. Analysis of ram ventilation of fish gills with application to skipjack tuna (*Katsuwonus pelamis*). J. Fish. Res. Bd. Can. **27**: 1637–1652.

Cameron, D., and Begg, G. 2002. Fisheries biology and interaction in the northern Australian small mackerel fishery. Final report to the Fisheries Research and Development Corporation for project no. 92/144. Department of Primary Industries, Brisbane, Australia.

Christensen, V., and D. Pauly. 1992. Ecopath II: a software for balancing steady-state ecosystem models and calculating network characteristics. Ecol. Model. **61**: 169–185.

Cowling, A., and Polacheck, T. 1995. Development of a fishery independent index of SBT abundance. Final report to the Fisheries Research and Development Corporation for project no. 94/149, CSIRO, Hobart, Australia.

Cox, S.P., Martell, S.J.D., Walters, C.J., Essington, T.E., Kitchell, J.F., Boggs, C., and Kaplan, I. 2002*a*. Reconstructing ecosystem dynamics in the central Pacific Ocean, 1952–1998. I. Estimating population biomass and recruitment of tunas and billfishes. Can. J. Fish. Aquat. Sci. **59**: 1724–1735.

Cox, S.P., Essington, T.E., Kitchell, J.F., Martell, S.J.D., Walters, C.J., Boggs, C., and Kaplan, I. 2002*b*. Reconstructing ecosystem dynamics in the central Pacific Ocean, 1952–1998. II. A preliminary assessment of the trophic impacts of fishing and effects on tuna dynamics. Can. J. Fish. Aquat. Sci. **59**: 1736–1747.

Cyrus, D.P., and Blaber, S.J.M. 1992. Turbidity and salinity in a tropical northern Australian estuary and their influence on fish distribution. Est. Coast. Shelf. Sci. **35**: 545–563.

Davis, T.L.O., and Stanley, C.A. 2002. Vertical and horizontal movements of southern bluefin tuna (*Thunnus maccoyii*) in the Great Australian Bight observed with ultrasonic telemetry. Fish. Bull. **100**: 448–465.

Domeier, M.L., and Dewar, H. 2003. Post-release mortality rate of striped marlin (*Tetrapterus audax*) caught with recreational tackle. Mar. Freshwater Res. **54**: 435–445.

Dotson, R.C. 1976. Minimum swimming speed of albacore, *Thunnus alalunga*. Fish. Bull. **74**: 955–960.

Dowis, H.J., Sepulveda, C.A., Graham, J.B., and Dickson, K.A. 2003. Swimming performance studies on the eastern Pacific bonito *Sarda chiliensis*, a close relative of the tunas (family Scombridae). II. Kinematics. J. Exp. Biol. **206**: 2749–2758.

Food and Agriculture Organization of the United Nations. 2005. Review of the state of world marine fishery resources. FAO Fish. Tech. Pap. No. 457.

© 2007 NRC Canada

Frid, C., Paramor, O., and Scott, C. 2005. Ecosystem-based fisheries management: progress in the NE Atlantic. Mar. Policy **29**: 461–469.

Gelman, A., Carlin, J.B., Stern, H.S., and Rubin, D.B. 2004. Bayesian data analysis. 2nd ed. Chapman and Hall, London, UK.

Gilks, W.R., Richardson, S., and Spiegelhalter, D.J. 1996. Markov chain Monte Carlo in practice. Chapman and Hall, London, UK.

Godinot, O., and Allain, V. 2003. A preliminary Ecopath model of the warm pool pelagic ecosystem. Working paper BBRG-5. *In* 16th Meeting of the Standing Committee on Tuna and Billfish, Mooloolaba, Australia, 9–16 July 2003. Secretariat of the Pacific Community, Noumea, New Caledonia.

Graves, J.E., Luckhurst, B.E., and Prince, E.D. 2002. An evaluation of pop-up satellite tags for estimating postrelease survival of blue marlin (*Makaira nigricans*) from a recreational fishery. Fish. Bull. **100**: 134–142.

Griffiths, S.P. 2001. Diel variation in the seagrass ichthyofaunas of three intermittently open estuaries in south-eastern Australia: implications for improving fish diversity assessments. Fish. Manag. Ecol. **8**: 101–118.

Griffiths, S.P., Fry, G.F., Manson, F.J., and Pillans, R.D. 2007. Feeding dynamics, consumption rates and daily ration of longtail tuna (*Thunnus tonggol*) in Australian waters: quantifying trophic interactions with a demersal prawn trawl fishery. Mar. Freshwater Res. **58**: 376–397.

Hall, S.J., and Mainprize, B. 2004. Towards ecosystem-based fisheries management. Fish Fish. **5**: 1–20.

Hamely, J.M. 1975. Review of gillnet selectivity. J. Fish. Res. Board Can. **32**: 1943–1969.

Hansson, S., and Rudstam, L.G. 1995. Gillnet catches as an estimate of fish abundance: a comparison between vertical gillnet catches and hydroacoustic abundances of Baltic Sea herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). Can. J. Fish. Aquat. Sci. **52**: 75–83.

Holland, K., Brill, R., and Chang, R.K.C. 1990. Horizontal and vertical movements of Pacific blue marlin captured and released using sportfishing gear. Fish. Bull. **88**: 397–402.

Ihaka, R., and Gentleman, R. 1996. R: a language for data analysis and graphics. J. Comput. Graph. Stat. **5**: 299–314.

Itoh, T., Tsuji, S., and Nitta, A. 2003. Swimming depth, ambient water temperature preference, and feeding frequency of young Pacific bluefin tuna (*Thunnus orientalis*) determined with archival tags. Fish. Bull. **101**: 535–544.

King, M. 1995. Fisheries biology, assessment and management. Blackwell Science, Oxford, UK.

Kitchell, J.F., Essington, T.E., Boggs, C.H., Schindler, D.E., and Walters, C.J. 2002. The role of sharks and longline fisheries in a pelagic ecosystem of the central Pacific. Ecosystems, **5**: 202–216.

Klimley, A.P., Jorgensen, S.J., Muhlia-Melo, A., and Beavers, S.C. 2003. The occurrence of yellowfin tuna (*Thunnus albacares*) at Espiritu Santo Seamount in the Gulf of California. Fish. Bull. **101**: 684–692.

Korsmeyer, K.E., and Dewar, H. 2001. Tuna metabolism and energetics. *In* Tuna physiology, ecology and evolution. *Edited by* B.A. Block and E.D. Stevens. Academic Press, San Diego, Calif. pp. 35–78.

Kuhnert, P.M., Martin, T.G., Mengersen, K., and Possingham, H.P. 2005. Assessing the impacts of grazing levels on bird density in woodland habitat: a Bayesian approach using expert opinion. Environmetrics, **16**: 717–747.

Lambert D. 1992. Zero-inflated Poisson regression with an application to defects in manufacturing. Technometrics, **34**: 1–14.

Lawless, J.F. 1987. Negative binomial and mixed Poisson regression. Can. J. Stat. **15**: 209–225.

Lutcavage, M., Kraus, S., and Hoggard, W. 1997. Aerial survey of giant bluefin tuna, *Thunnus thynnus*, in the Great Bahama Bank, Straits of Florida, 1995. Fish. Bull. **95**: 300–310.

Lyle, J.M. 1987. Northern pelagic fish stock research programme: summary of catch and effort data. Fishery Report No. 16. Fisheries Division, Department of Industries and Development, Northern Territory, Australia.

Lyle, J.M., and Timms, G.J. 1984. North Australia's multi-species shark fishery. Exploratory fishing survey of shark and other pelagic fish resources found in Northern Territory inshore waters. Fishery Report No. 12, Volume 4. Department of Primary Production, Darwin, Northern Territory, Australia.

McCullagh, P., and Nelder, J.A. 1989. Generalized linear models. 2nd ed. Chapman and Hall, New York.

Ménard, F., Stéquerta, B., Rubina, A., Herrerac, M., and Marchal, E. 2000. Food consumption of tuna in the equatorial Atlantic ocean: FAD-associated versus unassociated schools. Aquat. Living Resour. **13**: 233–240.

Musyl, M.K., Brill, R.W., Boggs, C.H., Curran, D.S., Kazama, T.K., and Seki, M.P. 2003. Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts near the main Hawaiian Islands from archival tagging data. Fish. Oceanogr. **12**: 152–169.

Myers, R.A., and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. Nature (London), **423**: 280–283.

Ohta, I., and Kakuma, S. 2005. Periodic behavior and residence time of yellowfin and bigeye tuna associated with fish aggregating devices around Okinawa Islands, as identified with automated listening stations. Mar. Biol. **146**: 581–594.

Okey, T.A. 2006. An Ecopath model of Albatross Bay, Gulf of Carpentaria, Australia, for the period 1986–1992: a contribution to the FRDC 2004/024 project "Variation in banana prawn catches at Weipa: a comprehensive regional study". Final report to the Fisheries Research and Development Corporation for project no. 2004/024. CSIRO, Cleveland, Australia.

Olson, R.J., and Boggs, C.H. 1986. Apex predation by yellowfin tuna (*Thunnus albacares*): independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. Can. J. Fish. Aquat. Sci. **43**: 1760–1775.

Olson, R.J., and Watters, G.M. 2003. A model of the pelagic ecosystem in the eastern tropical Pacific Ocean. Int.-Am. Trop. Tuna Com. Bull. Vol. 22, No. 3.

Pauly, D., Christensen, V., and Walters, C. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J. Mar. Sci. **57**: 697–706.

Pepperell, J.G., and Davis, T.L.O. 1999. Post-release behaviour of black marlin, *Makaira indica*, caught off the Great Barrier Reef with sportfishing gear. Mar. Biol. **135**: 369–380.

Plaganyi, E.E., and Butterworth, D.S. 2004. A critical look at the potential of Ecopath with Ecosim to assist in practical fisheries management. Afr. J. mar. Sci. **26**: 261–287.

Porch, C.E., Fisher, M.R., and McEachron, L.W. 2002. Estimating abundance from gillnet samples with application to red drum (*Sciaenops ocellatus*) in Texas bays. Can. J. Fish. Aquat. Sci. **59**: 657–668.

Royer, F., Fromentin, J.M., and Gaspar, P. 2004. Association between bluefin tuna schools and oceanic features in the western Mediterranean. Mar. Ecol. Prog. Ser. **269**: 249–263.

Rudstam, L.G., Magnuson, J.J., and Tonn, W.M. 1984. Size selectivity of passive fishing gear: a correction for encounter probability applied to gill nets. Can. J. Fish. Aquat. Sci. **41**: 1252–1255.

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Sambilay, V.C., Jr. 1990. Interrelationships between swimming speed, caudal fin aspect ratio and body length of fishes. Fishbyte, **8**: 16–20.

Scandol, J.P., Holloway, M.G., Gibbs, P.J., and Astles, K.L. 2005. Ecosystem-based fisheries management: an Australian perspective. Aquat. Living Resourc. **18**: 261–273.

Schaefer, K.M., and Fuller, D.W. 2002. Movements, behavior, and habitat selection of bigeye tuna (*Thunnus obesus*) in the eastern equatorial Pacific, ascertained through archival tags. Fish. Bull. **100**: 765–788.

Schick, R.S., Goldstein, J., and Lutcavage, M.E. 2004. Bluefin tuna (*Thunnus thynnus*) distribution in relation to sea surface temperature fronts in the Gulf of Maine (1994–96). Fish. Oceanogr. **13**: 225–238.

Serventy, D.L. 1956. Additional observations on the biology of the northern bluefin tuna, *Kishinoella tonggol* (Bleeker), in Australia. Aust. J. Marine Freshwater Res. **7**: 44–63.

Spiegelhalter, D.J., Best, N.G., Carlin, B.P., and Vander Linde, A. 2002. Bayesian measures of model complexity and fit (with discussion). J. R. Stat. Soc. Ser. B, **64**: 583–640.

Stevens, J.D., and Davenport, S.R. 1991. Analysis of catch data from the Taiwanese gill-net fishery off northern Australia, 1979 to 1986. CSIRO Mar. Lab. Rep. No. 213, Hobart, Australia.

Welsh, A.H., Cunningham, R.B., Donnelly, C.F., and Lindenmayer, D.B. 1996. Modelling the abundance of rare species: statistical models for counts with extra zeros. Ecol. Model. **88**: 297–308.

Appendix A. Sensitivity analysis

In our derivation of the probability that an animal encounters the net, we assumed that animals swim in a random, but constant, direction during the soak time of the gillnet. This assumption is unrealistic, but we expected that the abundance estimate would be fairly insensitive to this assumption in the sense that if the animal were to make a limited number of small random deviations from this fixed initial direction throughout the soak time, then the probability of encountering the net would not change markedly. In context, this would be a negligible perturbation of the model. Below we describe a simulation experiment designed to provide some justification of this contention.

We assume that the gillnet is of unit length and that fish encountering the net still swim with a fixed swimming speed. This swimming speed and the soak time of the net together determine the maximum distance from which a fish can swim and still have a chance of encountering the net, i.e., the domain of potential interaction. In terms of the symbols used in our paper, this maximum possible swimming distance is the ratio d/h. Rather than assume that fish swim strictly in a constant but random direction, we now allow fish to deviate from their current swimming direction according to a Poisson process. Initially each fish swims in a random direction. At a random time later, according to the Poisson process, the direction of swimming deviates from the current direction by a random angle distributed as $N(0, s^2)$. Let r be the rate parameter of the Poisson process, i.e., the average number of change events that occur in a single swimming trajectory while the net is in the water. The simulations proceed as follow. (*i*) A random location is chosen within the domain of potential interaction as the initial position of a fish when the net is set. (*ii*) When the net is set, the fish swims in a random direction, chosen as a uniform random variable on the range $-\pi$ to π. (*iii*) This initial direction persists for a time period chosen as an exponential random variable with rate parameter r, i.e., according to the gap time distribution for a Poisson process. (*iv*) At this point, the fish deviates its swimming direction by an angular quantity distributed as $N(0, s^2)$. (*v*) This process continues until either the animal encounters the net or has swum a distance of d/h, when the soak time is finished.

The same process is repeated a large number of times, $N = 10^6$, and the relative frequency of encountering the net is reported. This is then compared with the probability $p(d/h)$ as used in our paper.

The angular standard deviations (s, in degrees) considered are 0, 5, 10, and 20, and the average numbers of direction changes (r) are 0, 1, 5, 10, and 20 during the soak time. The maximum swimming distances (d/h) considered are 0.05, 0.1, 0.2, 0.5, and 1. These ranges were chosen to cover the principal region of interest in practice. The probabilities, under constant direction, range from about 0.1 to 0.3. Because the fish are swimming only to maintain buoyancy and oxygen supply to the gills, large numbers of abrupt changes in direction are considered unlikely.

Notice that when either $r = 0$ or $s = 0$, or both, the original assumption of a constant direction is maintained. This serves as a check on the simulation process itself and gives some indication of simulation variability in Table A1 (below) and Fig. A1 (next page).

The chance that an animal within the domain of potential interaction encounters the net, under the assumption of a constant direction, is given in Table A1. Figure A1 shows how these probabilities vary when the three parameters d/h, r, and s are changed. The results indicate that for modest increases in either parameter, the probability of encountering the net, $p(d/h)$ changes by only a small amount, as might be expected. Even with both $s = 20$ and $r = 20$, $p(d/h)$ is reduced by only about 10%, and we consider this scenario as probably outside the realistic practical situation.

Table A1. Probability of capture ($p(d/h)$) for different d/h scenarios.

d/h	1	0.5	0.2	0.1	0.05
$p(d/h)$	0.123976	0.178553	0.242721	0.275955	0.295949

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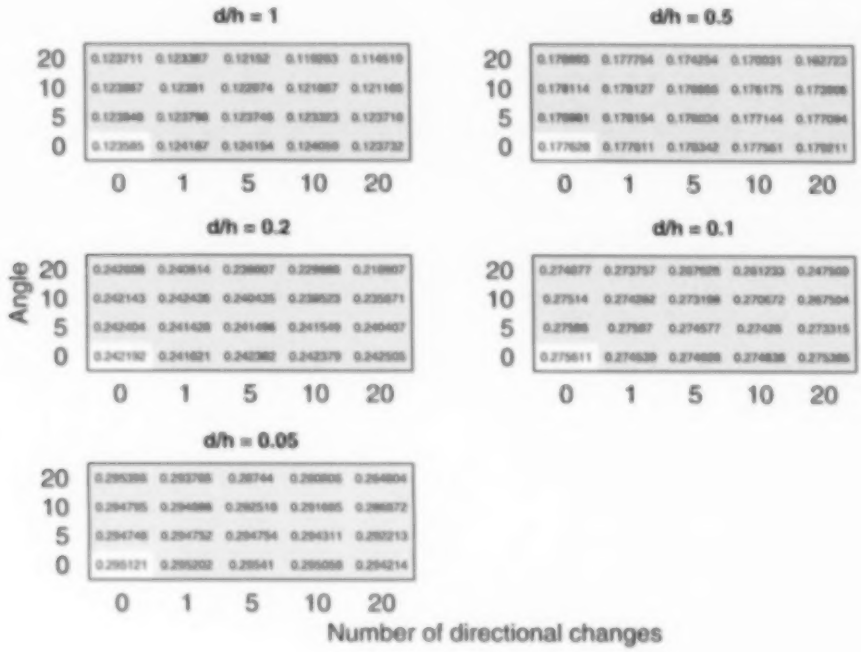
Fig. A1. Simulation-based estimates of the probability of encountering the net as a function of maximum swimming distance, *d*/*h*, average number of direction changes, *r*, and angular standard deviation of direction changes, *s*. The open cell should closely reflect the actual probabilities highlighted in Table A1. Other cells in the left-most column and bottom row of each table should also approximate these values.



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Metabolic rate and tissue reserves in gilthead sea bream (*Sparus aurata*) under thermal fluctuations and fasting and their capacity for recovery

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Abstract: To differentiate between cold and fasting effects on gilthead sea bream (*Sparus aurata*) physiology, three conditions (cold-induced fasting at 8 °C, cold group; forced fasting at 18 °C, fasting group, and cyclic thermal fluctuations between 16 °C and 8 °C, fluctuating group) were compared with a control group (feeding at 18 °C). Oxygen consumption rate, plasma lipid fractions, and tissue composition were analysed either during long exposure (5 weeks) or after 20 days of recovery. Sea bream showed strict thermoconformism in metabolic rate and feeding, and all groups, after changes, mobilised perivisceral fat. The fasting group also consumed other tissue reserves sequentially, except nonpolar lipids in liver. In the cold group, this liver lipid fraction increased twofold, but in the fluctuating group, food intake was gradually restored during each short period of higher temperature, and the steatotic livers caused by cold were not seen. During recovery, the fasting group showed the highest growth rate and deposition of reserves, whereas the cold group, although they mobilised liver lipid, did not grow. Appropriate management of the transient short periods of higher temperature may improve recovery from the cold season in gilthead sea bream culture.

Résumé : Afin de distinguer entre les effets du froid et du jeûne sur la physiologie de la daurade royale (*Sparus aurata*), nous avons comparé trois conditions expérimentales (jeûne provoqué par le froid à 8 °C, groupe au froid; jeûne forcé à 18 °C, groupe à jeun; fluctuations thermiques cycliques entre 16 °C et 8 °C, groupe fluctuant) à une situation témoin (groupe alimenté à 18 °C). Nous avons analysé le taux de consommation d'oxygène, les fractions lipidiques du plasma et la composition des tissus soit au cours d'une longue exposition (5 semaines), soit après 20 jours de récupération. Les daurades affichent un strict conformisme thermique dans leur taux métabolique et leur alimentation et tous les groupes, après les changements, mobilisent leurs graisses périviscérales. Le groupe à jeun utilise une séquence d'autres réserves tissulaires, à l'exception des lipides non polaires du foie. Chez le groupe au froid, cette fraction lipidique du foie double, alors que l'ingestion de nourriture chez le groupe fluctuant est rétablie durant chaque période courte de chaleur et il ne se développe pas de stéatose du foie due au froid. Durant la récupération, le groupe à jeun connaît le taux le plus élevé de croissance et de dépôt de réserves, alors que le groupe au froid ne fait aucune croissance, même s'il mobilise ses lipides hépatiques. Une gestion appropriée des courtes périodes transitoires de chaleur peut améliorer la récupération de la saison froide dans les cultures de daurades royales.

[Traduit par la Rédaction]

Introduction

The use of energy by fish depends on both life history and environment. Knowledge of the mechanisms that fish use to survive periods of food deprivation and the consecutive recovery period would contribute to enhancing aquaculture production. Feed intake of gilthead sea bream (*Sparus aurata*) cultured in the northern Mediterranean coasts decreases or ceases during cold season. Consequently, fish growth is halted or greatly reduced during an unproductive period that may extend from November to April (Tort et al. 1998). Moreover, associated with natural cold periods in those latitudes appears a pathology, known as "winter disease", exclusively affecting cultured gilthead sea bream. This complex phenomenon involves several factors such as low temperatures, stress, metabolic depression, immune suppression, and eventual opportunistic pathogens (review in Tort et al. 2005), and cold condition may be responsible for all the factors (except pathogens) affecting the physiology of gilthead sea bream.

As in other poikilotherms, falls in temperature slow the metabolism of fish. Although compensatory responses have been demonstrated in many fish, the oxygen consumption rate of gilthead sea bream submitted to 8 °C for 20 days reveals lack of acclimation (Ibarz et al. 2003). Gilthead sea bream do not feed below 13 °C (Ibarz et al. 2003), and fish

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maintained at low temperatures deposit large amounts of lipids from other tissues in liver, resulting in tissue and metabolic alterations (Sala-Rabanal et al. 2003; Ibarz et al. 2005, 2007). Mobilisation and use of energy depots in food-deprived animals vary according to species, environment, and period studied. There are few studies on the effects of fasting in gilthead sea bream, but Power et al. (2001) observed that this species, after fasting for 3 weeks at 14 °C, mobilised body stores, including liver lipids. In addition, Grigorakis and Alexis (2005) showed that liver mass decreased in fasted gilthead sea bream at 24–28 °C. At the onset of spring or end of winter, when cultured gilthead sea bream resume feeding, peaks of heavier mortality occur (Padrós et al. 1996; Sarusic 1999), indicating that recurrent thermal fluctuation subjects fish to repetitive stress and metabolic challenge.

The aim of the present study was to differentiate among the effects of low temperatures, forced fasting, and repetitive thermal stress in gilthead sea bream during long-term exposure. Energy cost and use of reserves in each condition were studied from oxygen consumption rates and tissue composition changes, respectively. Plasma and liver lipid fractions, reflecting mobilisation and use of fat stores, were also analysed. A period of reversion to the initial condition was included to assess the recovery capacity of this species.

Material and methods

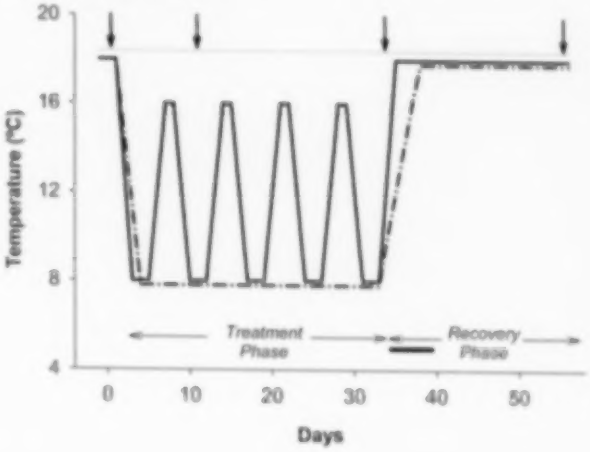
Fish

Gilthead sea bream (initial weight over 100 g) from a local fish farm were acclimated indoors at the Centre d'Aqüicultura (CA-IRTA, Sant Carles de la Ràpita, Tarragona, Spain) at 18 °C for 2 months. They were then randomly distributed in four experimental groups and reared for 1 additional month (50 fish per tank; density, 2.5–3 kg·m^{-3}; weight (mean ± standard error of the mean (SEM)), 144.2 g ± 4.8 g). We used 2 m^3 tanks that were connected to a semi-closed system with solid and biological filters and ozone protein skimmers and supplied with aerated seawater (3.8‰) that was partially sterilised with UV light. Water temperature, oxygen concentration, and water flow were controlled automatically. Water quality was controlled throughout the experimental period, maintaining nitrite, nitrate, and ammonia concentrations at initial values. Dissolved oxygen never fell below 7.5 mg·L^{-1}, and pH was maintained at over 8.0. Fish were fed a commercial diet (Mistral 3 mm, ProAqua, Dueñas, Spain) once a day to apparent satiation. Diet composition was 47% protein, 21% lipids, 11% ash, 1.5% fibre, and 19.8 MJ·kg^{-1} digestible energy.

Experimental design

A representation of the trial, performed during March and April, is provided (Fig. 1). In the first 35 days, called treatment phase, fish were submitted to four experimental rearing conditions: two groups were maintained at 18 °C with (control) or without (fasting) food. A third group (cold) was subjected to a water temperature decrease from 18 °C to 8 °C in 3 days and then maintained at 8 °C until day 35. Finally, the fourth group (fluctuating) was subjected to five repetitive thermal fluctuations as follows: a thermal shift from 18 °C to 8 °C in 1 day, maintenance at 8 °C for 3 days, a thermal increase from 8 °C to 16 °C in 1 day, and then maintenance at 16 °C for 2 days more. This sequence of events was repeated five times (see Fig. 1). Although both cold and fluctuating groups were fed, fish did not eat when the temperature fell below 12 °C. After 35 days of treatment phase, the recovery phase began by returning all groups gradually to the initial temperature and (or) feeding conditions during 5 days. Fish were then kept for 15 additional days under these conditions. No mortality occurred throughout the experimental period (treatment and recovery phases). Water temperature was adjusted with precision using external cooling units (EA-2001, CUBIJEI, Bologna, Italy) in conjunction with the internal thermal control of the system. All fish handling procedures complied with Spanish guidelines for animal care.

Fig. 1. Experimental design: treatment phase, application of experimental conditions, from day 0 to 35; recovery phase, from day 36 to 55. Arrows indicate samplings (days 0, 12, 35, and 55). Solid bar in recovery phase indicates the gradual re-establishment of initial temperature and (or) feeding conditions. Control and fasting, solid grey line; fluctuating, solid black line; cold, dashed–dotted line.



Sampling and analysis

Initial control samples (day 0) were obtained from 10 fish randomly selected from the four tanks before treatments. Samples from 10 fish per group (fasting, cold, and fluctuating) were obtained after 12, 35 (treatment phase), and 55 days (end of recovery phase). Ten fish from the control group were sampled at day 55 for comparison. Body weight and length were measured, fish were killed by severing their spinal cord, and blood samples were taken from the caudal vessels, using ethylenediaminetetraacetic acid – lithium (EDTA-Li) as anticoagulant. Plasma was obtained by centrifuging the blood for 5 min at 13 000*g* and 4 °C and then kept at –80 °C until analysis. Perivisceral fat (all the whitish mass surrounding the gut) and liver weights were also recorded, and samples of liver and epaxial white muscle were immediately frozen and stored at –80 °C.

Protein content was estimated on the basis of elemental nitrogen, burning samples in an elemental CHN analyser

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(EA 1108 CHNS-O, Carlo Erba Instruments, Milano, Italy). A correction factor of 6.25 (grams protein per gram nitrogen) was used to convert elemental nitrogen to protein. Total lipid content was purified following the method of Folch et al. (1957). After two extractions with chloroform–methanol (2:1 by volume), lipid extracts were purified, dried on a Rotavap (Büchi Rotavapor 4–114, Büchi Labortechnik AG, Flawil, Switzerland), and weighed. Crude lipid samples were separated into polar and nonpolar fractions by silica Sep-Pak cartridges (Waters, Milford, Mass.) using chloroform, chloroform–methanol (49:1 by volume), and methanol as solvents (Juaneda and Rockelin 1985). Fatty acid methyl esters from each lipid fraction were prepared, according to Christie's method (1982), by a 50 °C and 16 h acid-catalysed transmethylation, and then were extracted and purified following Tocher and Harvie (1988). Details of the chromatography procedure and fatty acid identification (by gas chromatograph (Carlo Erba GC 8000 Top) and mass spectrometer (Fisons MD-800)) are described elsewhere (Ibarz et al. 2005). Glycogen from tissue samples was purified after alkaline-hydrolysis extraction and alcoholic precipitation, and the content of extracts was determined by the colorimetric reaction of carbohydrates with anthrone – sulfuric acid, using mussel glycogen as standard (Fraga 1956).

Plasma aliquots were diluted with phosphated buffered saline to 1/20 for triglyceride (TAG), phospholipid (PL), and total cholesterol (TC) analysis or 1/10 for nonesterified fatty acid (NEFA) analysis. Plasma TAG concentrations were obtained according to the successive enzymatic reactions of lipoprotein lipase, glycerol kinase, glycerol phosphatase–oxidase, and glycerol phosphatase–peroxidase (McGowan et al. 1983); plasma PL were hydrolysed by phospholipase D, and the liberated choline was measured by the Trinder reaction using choline oxidase and peroxidase; TC by cholesterol hydrolase and cholesterol oxidase colorimetric method (Allain et al. 1974); and NEFA by transformation to their Cu–NEFA complexes (Itaya and Ui 1965). For each determination, a commercial diagnosis kit was adapted to a microplate procedure, previously validated, and all the data fell within the linearity range of the kit (TAG, GPO-Trinder, Sigma; PL, MPR-2, Roche-Boehringer; TC, TC-kit, Medical Analysis System; NEFA, NEFA-C, Wako Chemicals). Concentrations of TAG, PL, and TC are expressed as mg fraction·dL^{-1} and NEFA is expressed as mequiv.·dL^{-1}.

Oxygen consumption measurements

To measure oxygen consumption, two 70 L metabolic chambers were connected to each maintenance system by a siphon and a recirculation water pump, as described by Ibarz et al. (2003). Measurements of oxygen intake were taken in two periods: between days 5 and 10 (short exposure) and between days 30 and 35 (long exposure). Three fish were placed in the metabolic chamber the night before measurements. Changes in oxygen content in the chamber were recorded for periods of 45–60 min. Fish in the cold and fasting treatments were not fed from the beginning of the experiment, whereas fish in the control and fluctuating groups were previously fasted for 24 h in an attempt to avoid possible food effects. After the measures were obtained, fish were netted, lightly anaesthetised, and weighed, the chambers were cleaned, and another three fish were placed in the chamber for acclimation.

Orion M-835 oxygen electrodes (Thermo Electron Corp., Madison, Wis.) were calibrated before each measurement, and each electrode was placed into the chamber and provided with a constant water flow on the tip to stabilize the measure. The chamber was closed, and all the connections were sealed. The oxygen meters provided dissolved oxygen levels (in mg O_2·L^{-1} and percent saturation), and the values were corrected according to water salinity (3.8‰). The decay of the oxygen levels always exceeded 0.5 ppm, and the oxygen saturation levels in the chamber never fell below 70%. These conditions assured an adequate measurement of the oxygen consumption of fish.

The thermal coefficient (Q_{10}) of metabolic rates was calculated using the formula of Prosser (1991):

$$Q_{10_{t_1 \to t_2}} = (K_2/K_1)^{10/(t_2 - t_1)}$$

where K_1 and K_2 are the mean of oxygen consumption rates at temperatures t_1 (initial) and t_2 (final), respectively (see data in Table 1).

Statistics

Results are presented as the mean ± SEM. Statistical differences of variables were analysed by one-way analysis of variance (ANOVA). When significant, differences among each treatment were analysed by post-hoc tests (Tukey when variances were homogeneous, or Dunett-T3 when variances were nonhomogeneous). These tests were applied at a significance level of $p < 0.05$. All statistical analyses were performed using SPSS v.12 (SPSS Inc., Chicago, Illinois).

Results

Animal activity

During a short exposure (days 5 to 10 of the experiment), the aerobic metabolic rate decreased after food withdrawal (fasting group) and cold shifts (both cold and fluctuating groups; see Table 1). The Q_{10} of oxygen consumption rates after the thermal shift from 18 °C to 8 °C were 2.4 and 2.6 for cold and fluctuating groups, respectively. These values are within the range of strict thermoconformism (i.e., metabolic depression directly proportional to the temperature drop without compensatory responses). In long exposure, the fasting group showed a slight increase in oxygen intake. After 5 weeks at low temperature, oxygen consumption was 25% greater than after short exposure. However, this increase may be due to a slight increase in water temperature from 8 °C to 11 °C during the final period of measurement. The physiology and behaviour of fish exposed to thermal fluctuations varied in response to water temperature. Thus, during periods at 8 °C, they did not feed and showed minimal activity; however, at 16 °C, their swimming and feeding activities was apparently normal. In detail, the thermal fluctuating group accepted increasing amounts of food at each warm-up period (first, 23% of the ration taken by fish at a constant temperature for 16 °C; second, 38%; third, 53%; fourth, 75%). After both falls (18 to 8 °C) and rises (8 to 16 °C) in temperature, the Q_{10} values of oxygen consumption levels in the fluctuating group were always between 2

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Table 1. Effects of treatments on the oxygen consumption of gilthead sea bream.

Treatment[a]	Time interval[b]	Temperature (°C)	Oxygen consumption (mg $O_2 \cdot kg^{-1} \cdot h^{-1}$)
Control	Short exposure	17.8±0.2	263.8±8.6a
	Long exposure	20.4±0.1	259.6±9.8a
Fasting	Short exposure	17.2±0.1	194.4±9.7b
	Long exposure	18.5±0.3	235.1±5.6a
Cold	Short exposure	8.2±0.1	119.1±7.4c
	Long exposure	10.9±0.1	159.9±6.7d
Fluctuating	Initial	16.8±0.2	263.5±21.9a
	1st shift	10.5±0.1	142.0±5.45b
	1st rise	17.2±0.1	238.9±7.88a
	2nd shift	9.6±0.1	129.3±6.01b
	5th shift	9.8±0.1	127.2±15.5b
	5th rise	17.9±0.1	259.6±15.5a

Note: Oxygen consumption values in mean ± standard error of the mean.

[a]Statistical differences were obtained among control, fasting, and cold groups together and in the fluctuating group alone. Means with different letters are significantly different ($p < 0.05$).

[b]Time interval indicates the period during which the measurements were done (for further details see the methods section). $n > 10$ in all cases.

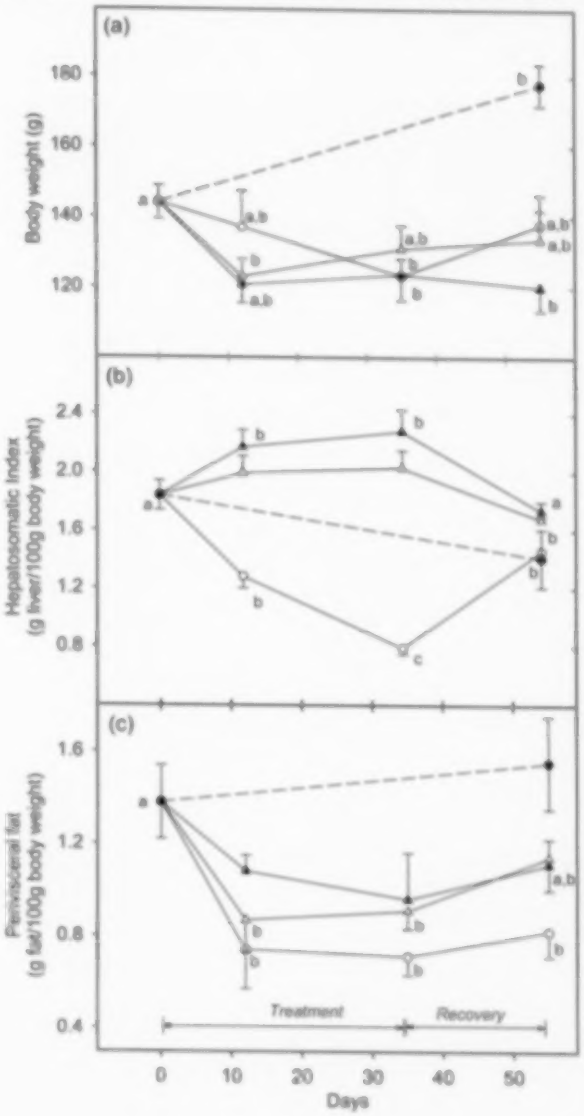
and 2.5 (first drop, 2.6; first rise, 2.2; second drop, 2.2; fifth drop, 2.5; fifth rise, 2.5). Even after long exposure, the observed dependence of metabolic expenditure on the temperature reaffirms that this species does not acclimatise to the cold.

Treatment phase

Changes in body weight, hepatosomatic index (HSI), and perivisceral fat are shown (Fig. 2). Control fish maintained for 55 days at 18 °C showed 20% increase in body weight, and total length rose from 20.9 ± 0.2 cm to 23.1 ± 0.2 cm. The percentage of perivisceral fat mass did not vary significantly (Fig. 2*c*). Experimental conditions had a distinct effect on body indices. Fasting at 18 °C provoked gradual losses in body and liver weights, whereas a thermal drop to 8 °C caused an acute decrease in the former. Liver of fish at 8 °C had a steatotic appearance (yellowish, fatty, and friable) and its mass did not decrease, and consequently, the HSI of this group increased significantly (Fig. 2*b*). The response of the fluctuating group was similar to that of the cold group, although the changes in the former were not as marked and the liver appeared to be normal. The highest mobilisation of perivisceral fat occurred in the fasting group, whereas the lowest was detected in fish kept at 8 °C. Thus, the amount of perivisceral fat used at day 12 showed a direct relationship to the oxygen consumption rate.

Glycogen, lipid, both polar and nonpolar fractions, and protein contents of total liver mass are shown (Fig. 3). After 55 days, control group presented significantly lower liver protein and nonpolar lipid levels than initial values. When fish were fasted, liver glycogen was used early and was almost depleted by day 35, followed by a significant decrease in liver protein. Hepatic nonpolar lipid content did not change significantly during food deprivation. Changes in liver composition differed between the cold and fluctuating

Fig. 2. Effects on (*a*) body weight, (*b*) hepatosomatic index, and (*c*) percent of perivisceral fat. Values are mean ± standard error of the mean ($n = 10$). Significant differences ($p < 0.05$) in each condition are indicated by different letters. Control, solid circles; fasting, open circles; cold, solid triangles; fluctuating, open triangles.



groups. Thus, liver lipid levels of the former had already increased in the nonpolar fraction at day 12 and also in the polar fraction at day 35, but the fluctuating group did not present lipid deposition in liver. White muscle lipid contents are shown (Fig. 4). Data on the other main components (protein and glycogen) are not included, because muscle protein ranged from 20% to 21% of tissue wet weight and did not significantly modify under any treatment and glycogen levels did not surpass 0.5% in any case. Lipid content of white muscle, in contrast to that of liver, decreased by half in fast-

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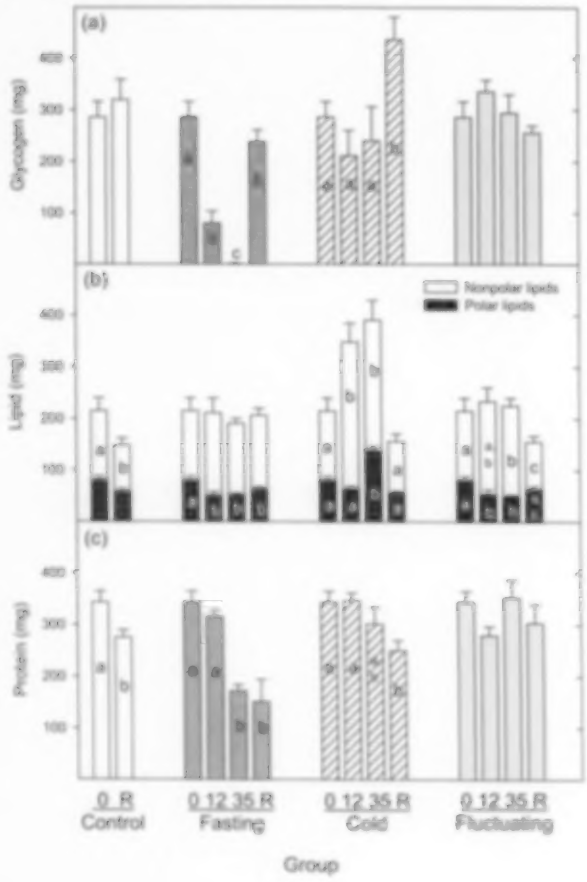
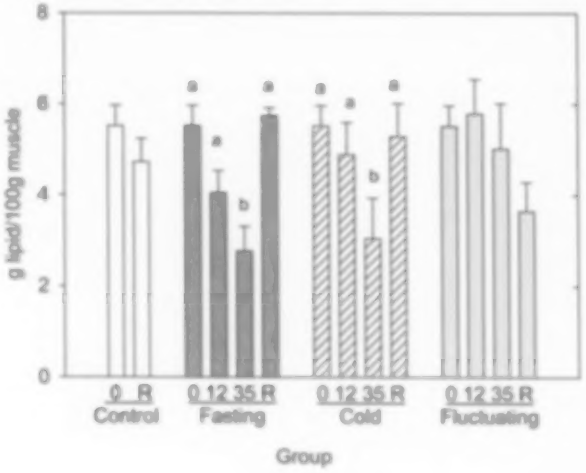
Fig. 3. Effects of experimental conditions on liver composition. Values are mean ± standard error of the mean of total liver mass (n = 10). The numbers 0, 12, and 35 correspond to the samplings during the treatment phase, and *R* corresponds to the sampling at the end of the recovery phase (day 55). Significant differences for polar and nonpolar lipids, glycogen, and protein in each condition ($p < 0.05$) are indicated by different letters.



ing and cold groups at day 35, whereas muscle lipids of the fluctuating group were maintained.

Fatty acid profiles of liver nonpolar and polar lipids are provided (Table 2). No significant changes were observed at day 12 for any group, and for clarity these data have not been included. In the control group, oleic acid (18:1 (n-9)) among nonpolar lipids and oleic, estearic (18:0) and eicosapentaenoic (EPA, 20:5 (n-3)) acids among polar lipids decreased significantly throughout the experiment, whereas the percentage of palmitic acid (16:0) increased. After 35 days of fasting, the total lipid content of liver did not change, but fatty acid profiles were significantly modified. In the nonpolar fraction, fatty acids with higher oxidation rates, such as oleic and estearic acids, decreased significantly, whereas docosahexaenoic acid (DHA, 22:6 (n-3)), one of the essential n-3 HUFAs, increased. In contrast, the variations observed in the fatty acid profile of polar lipids were not clearly related to the fasting condition. Thus, EPA and

Fig. 4. Effects of experimental conditions on muscle lipids. Values are mean ± standard error of the mean (n = 10). The numbers 0, 12, and 35 correspond to the samplings during the treatment phase, and *R* is the sampling at the end of the recovery phase (day 55). Significant differences in each condition ($p < 0.05$) are indicated by different letters.



linoleic acid (18:2 (n-6)) decreased, and palmitic and araquidonic (ArA, 20:4 (n-6)) acids increased. Lipid deposition in the liver of the cold group conditioned the rise of all fatty acids, in both nonpolar and polar fractions (see Fig. 3*b*). DHA showed the highest accumulation ($p < 0.05$), whereas palmitic and oleic acids reduced their percentage in the nonpolar fraction at day 35. Under repetitive thermal changes, the liver fatty acid profile of nonpolar lipids changed. DHA and linoleic acid increased, whereas palmitic and estearic acids decreased. No significant alterations in the profile of polar fatty acids in response to thermal fluctuations were observed.

Plasma levels of lipid fractions of control group at day 0 were as follows: TAG, 255 ± 17 mg·dL^{-1}; PL, 428 ± 47 mg·dL^{-1}; TC, 204 ± 7 mg·dL^{-1}, and NEFA, 1.16 ± 0.08 mequiv.·dL^{-1}; and after 55 days, levels did not change significantly. In the other three groups, the plasma levels of PL and TC (not shown) were not modified significantly. However, a transitory increase in plasma NEFA levels parallel to the depletion of perivisceral fat occurred in the cold and fluctuating groups (Fig. 5), although the fasting group showed no increase. The greatest variation in plasma lipid levels was for TAG, which doubled ($p < 0.05$) at day 12 in the cold and fluctuating groups. High TAG levels occurred at day 35 only in the latter, but decreased in the cold group ($p < 0.05$), indicating a distinct lipid export capacity from the liver between these two groups.

Recovery phase

We also evaluated the recovery capacity of this species after prolonged exposure to fasting, cold, and thermal fluctuations. All experimental groups showed normal swimming activities and organ appearance at the end of the recovery period but did not reach the final weight of control group. Body and liver weights of fasted fish recovered 95% and

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Table 2. Principal fatty acids contents of liver nonpolar and polar lipid fractions.

	Control (18 °C)		Fasting		Cold		Fluctuating	
	Day 0	Day 55	Treatment, day 35	Recovery, day 55	Treatment, day 35	Recovery, day 55	Treatment, day 35	Recovery, day 55
Nonpolar								
16:0	17.3±0.3	18.6±0.2	18.0±0.3	17.8±0.4	15.4±0.5*	17.6±0.3	14.7±0.2*	16.6±0.6
18:0	4.3±0.1	4.1±0.2	2.5±0.1*	4.3±0.2	3.8±0.2	5.2±0.2*	2.7±0.2*	4.4±0.1
Saturated	22.8±0.4	24.0±0.3	22.0±0.4	23.4±0.4	20.4±0.6*	23.9±0.5	18.3±0.1*	22.6±0.7
18:1 (*n*-9)	28.5±0.8	24.3±0.5*	23.2±0.3*	26.4±0.6	25.3±0.5*	26.9±0.5	24.5±0.3	27.4±0.6
Total *n*-9	41.5±1.0	35.7±0.7*	33.2±0.5*	38.0±0.6	39.0±0.4*	38.8±0.6	38.1±0.8	40.2±0.8
20:5 (*n*-3)	7.5±0.4	7.7±0.2	5.7±0.1	7.6±0.3	7.4±0.2	7.8±0.2	7.4±0.3	7.1±0.2
22:6 (*n*-3)	15.8±1.4	17.9±0.8	27.0±1.2*	17.8±0.6	18.8±0.7*	15.7±0.7	22.6±0.8*	15.6±0.3
n-3 HUFA	22.6±1.1	25.6±0.8	32.2±0.9*	25.4±0.8	25.2±1.4	23.5±0.7	30.0±0.9*	23.0±0.4
Total *n*-3	23.3±1.1	26.2±0.8	32.8±0.9*	25.8±0.9	25.9±1.4	24.1±0.7	30.7±0.9*	23.1±0.6
18:2 (*n*-6)	6.5±0.3	6.9±0.2	6.8±0.5	7.2±0.2	7.8±0.1	6.7±0.2	7.9±0.1*	7.7±0.3*
20:4 (*n*-6)	0.7±0.0	0.8±0.0	0.6±0.0	0.8±0.0	0.8±0.0	0.8±0.0*	0.7±0.0	0.8±0.0*
Total *n*-6	7.8±0.3	8.0±0.2	7.9±0.2	8.4±0.2	9.4±0.2	8.0±0.2	9.2±0.1*	9.2±0.3*
Unsaturated/saturated	3.4±0.1	3.2±0.1	3.6±0.1*	3.3±0.1	3.4±0.1	3.2±0.1	4.5±0.0*	3.2±0.1
Polar								
16:0	19.5±0.5	21.6±0.3*	21.1±0.3*	21.1±0.4*	20.4±0.2	19.8±0.2	20.5±0.4	20.1±0.4
18:0	8.4±0.2	7.6±0.2*	7.8±0.2	8.3±0.2	7.6±0.1*	9.0±0.3	7.3±0.2*	9.0±0.3
Saturated	29.1±0.4	30.5±0.3	30.2±0.5	30.9±0.2*	29.4±0.2	30.1±0.3	29.0±0.5	30.6±0.4
18:1 (*n*-9)	8.0±0.3	6.6±0.1*	8.3±0.4	7.4±0.1	7.5±0.3	7.7±0.1	7.7±0.3	7.7±0.1
Total *n*-9	11.5±0.3	10.8±0.1	12.6±0.5	11.3±0.1	11.1±0.2	11.5±0.2	11.9±0.3	11.8±0.2
20:5 (*n*-3)	13.5±0.3	12.2±0.3*	8.5±0.3*	11.6±0.2*	11.8±0.2*	11.4±0.1*	13.8±0.5	11.6±0.4*
22:6 (*n*-3)	35.8±0.9	36.8±0.4	37.3±0.8	36.6±0.2	37.6±0.6	36.7±0.5	34.8±1.2	35.5±0.5
n-3 HUFA	49.3±0.6	49.0±0.4	46.3±0.4*	48.1±0.3	48.6±0.3	48.3±0.5	47.8±0.6	46.7±0.4
Total *n*-3	52.2±0.6	50.3±1.2	49.4±0.3*	50.6±0.3	52.2±0.4	51.0±0.5	51.2±0.4	50.2±0.6
18:2 (*n*-6)	2.5±0.1	2.2±0.1	2.8±0.1*	2.3±0.0	2.2±0.1	2.2±0.0	2.6±0.1	2.3±0.1
20:4 (*n*-6)	2.8±0.1	3.0±0.1	3.2±0.1*	3.0±0.1	2.7±0.2	3.1±0.1	3.0±0.2	3.1±0.1
Total *n*-6	5.5±0.1	5.4±0.2	6.1±0.2*	5.6±0.1	5.4±0.2	5.5±0.1	5.8±0.1	5.7±0.1
Unsaturated/saturated	2.4±0.1	2.3±0.0	2.5±0.0	2.4±0.0	2.3±0.0	2.2±0.0	2.5±0.1	2.3±0.1

Note: Values are means ± standard error of the mean of percentages of total fatty acid mass. An asterisk (*) indicates a significant difference ($p < 0.05$) with respect to day 0 ($n = 5$).

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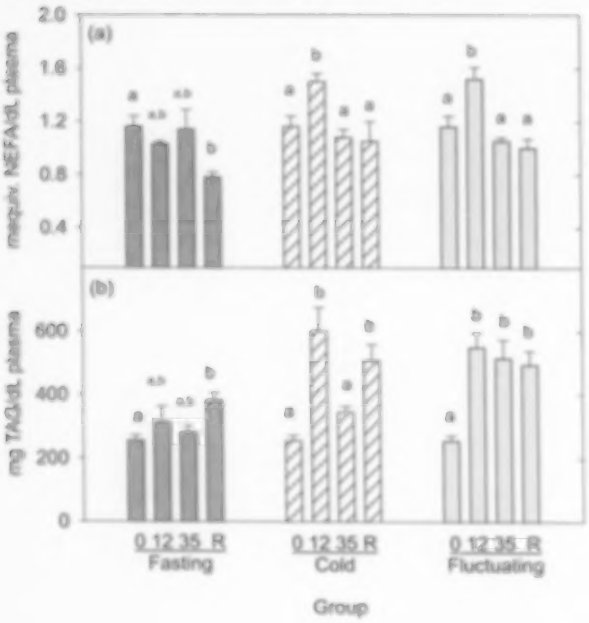
Fig. 5. Evolution of plasma concentration of (*a*) NEFA and (*b*) TAG. Values are mean ± standard error of the mean ($n = 10$). The numbers 0, 12, and 35 correspond to the samplings during the treatment phase, and *R* is the sampling at the end of the recovery phase (day 55). Significant differences for each reserve in each condition ($p < 0.05$) are indicated by different letters.



80% of the respective initial values (Fig. 2). In cold group, although the rise of temperature and restart of feeding reduced HSI values, growth was arrested during the 20-day recovery period. Most of the main changes observed in liver and muscle composition of the fasting and cold groups (Figs. 3 and 4) reverted at the end of the recovery period. Thus, in the former, liver glycogen and muscle lipid content recovered rapidly and in the cold group mobilised the accumulated hepatic lipids, having an overshoot of glycogen. Nevertheless, liver protein content was not re-established in either condition. The levels of most fatty acids were restored at the end of the recovery phase in all treatments (Table 2). Finally, NEFA levels decreased in the fasting group at day 55, whereas all the treatments showed higher plasma TAG levels than initial values (Fig. 5). The fish in the fluctuating group also showed greater recovery capacity than the cold group: fish growth began early, re-establishment of reserves was not necessary, and it was the only group that accumulated energy excess as perivisceral fat.

Discussion

Here we studied the effects of repetitive thermal fluctuations, simulating natural variations that may occur during winter and spring, on the mobilisation of hepatic and muscular energy reserves in gilthead sea bream. We compared these effects with those induced by long-term exposure to 8 °C and forced fasting at 18 °C. Our results indicate that fasted gilthead sea bream show sequential use of energy. Liver glycogen was mobilised early, which is consistent with reports for several species of teleostean fish (Sheridan and Mommsen 1991; Navarro et al. 1992; Collins and Anderson 1995), including gilthead sea bream (Power et al. 2001). During food deprivation, mesenteric fat was gradually mobilised, which is similar to findings reported in fish farms (Grigorakis and Alexis 2005). The fasting group showed delayed lipid muscle and liver protein use when food deprivation was prolonged and early reserves began to deplete. A loss of muscle mass, which can be inferred from the 16% reduction in body weight, also indicates a gradual use of muscle protein as observed in other species (Blasco et al. 1992; van Dijk et al. 2005). Fasting also reduces global activity, measured as oxygen consumption (Beamish 1964; Du Preez et al. 1986; Lemarié et al. 1992), which was clearly observed in this study.

Our data indicate that gilthead sea bream not only mobilises liver glycogen (Power et al. 2001; Metón et al. 2003) but, when necessary, can deplete this reserve. Thus, carbohydrate metabolism may acquire greater importance in feeding, as recently proposed by Venou et al. (2003) on the basis of digestibility and conversion efficiency. Moreover, we observed that the maintenance of the nonpolar lipid stores in total liver mass led to an increase in the percentage of this tissue component. This finding, which, to our knowledge, has not been reported in fasted fish, is contrary to the lipid use detected in other food-deprived fish, e.g., Atlantic cod (*Gadus morhua*; Guderley et al. 2003), golden perch (*Perca flavescens*; Foster and Moon 1991), carp (*Cyprinus carpio*; Blasco et al. 1992), and roach (*Rutilus rutilus*; van Dijk et al. 2005). In gilthead sea bream fasted for 3 weeks, Grigorakis and Alexis (2005) proposed that HSI losses indicate hepatic fat mobilisation; however, our data point to the use of protein and, mainly, glycogen liver depots. Our results cannot exclude the hepatic use of lipids during food deprivation, because fish fasted for 35 days mobilised oleic and estearic acids, while they maintained essential fatty acids, such as DHA. Lipogenesis should be reduced during fasting, as suggested by Bastrop et al. (1991). Although we did not measure lipogenesis, the lack of an increase in saturated nonpolar fatty acids is consistent with this hypothesis. Mesenteric fat mobilisation, without changes of plasma NEFA levels, and mainly the increment of essential fatty acids in liver support the idea that part of the lipid depots were of extrahepatic origin. This exceptional imbalance between input and output of lipids in the liver of fasting group (at 18 °C) was particularly evident when fish were kept at low temperatures. Depressed metabolism at 8 °C reduced the overall use of released lipids from perivisceral fat, as indicated by the increase of plasma NEFA levels. This may explain the greater lipid deposition observed in liver of fish kept at low temperatures (Ibarz et al. 2005, 2007; present study). We hypothesise that the acute mobilisation of lipids from mesenteric fat in response to fasting or cold stress conditions interferes with hepatic lipid metabolism. The mechanisms affected are still unclear, but the high levels of dietary PUFA (14.9% of total fatty acids, with a lipid content of 21% in dry weight) may alter lipid metabolism in liver.

Although most of the effects observed in the cold group occurred within a few days, which is consistent with previous observations (Gallardo et al. 2003; Ibarz et al. 2005, 2007), the maintenance of gilthead sea bream at 8 °C for

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35 days (long exposure) had only minor effects. This confirms that the stress associated with the thermal shift is the main cause for cold-induced changes, and the long exposure under such temperatures does not aggravate cold sea bream condition, although it does not improve it either. Only the increase in liver polar lipids indicated a possible acclimation of liver membranes, which has also been reported in other species (Hazel 1984; Dey et al. 1993). Two processes, cell hyperplasia and organelle proliferation, could explain the polar lipid increase as demonstrated for muscle (Egginton and Sidell 1989; Riemenschneider and Sidell 2002; Guderley 2004). However, these processes have not been examined in liver.

Gilthead sea bream show strict thermoconformism (Ibarz et al. 2003), and this response was also found under cyclic thermal shifts. After 5 weeks, the changes in oxygen consumption demonstrated that the fluctuating group did not acclimate to repetitive thermal shifts. The effects of stress caused by cold did not increase when temperature drop was repeated, even after five cycles. Although fish were active and feeding for very short periods, they compensate for the damage caused by longer cold intervals. Fat mobilisation by thermal stress occurred, but hepatic lipid content did not increase because the export of these lipids from liver as TAG (according to Sheridan 1988) was constant during thermal fluctuations, as shown by higher plasma levels. Wallaert and Babin (1994) suggested that a sign of cold adaptation in trout is the export of lipids from liver as lipoprotein, causing persistent hypertriglyceridemia. Under long exposure, this effect was observed in the fluctuating group, but not in the cold group. The reduced lipid export, which may be related to alterations of lipoprotein metabolism, and the reduction of hepatic protein synthesis previously reported (Sala-Rabanal et al. 2003) can explain the lack of adaptation of gilthead sea bream to cold.

During recovery from food deprivation, fish present various recovery dynamics (reviewed by Ali et al. 2003). Full compensation on growth, defined as restoration of the same values as those shown by the nonrestricted group, was not observed in any experimental condition. Eroldogan et al. (2006), assaying growth and feed intake of gilthead sea bream in response to symmetrical and asymmetrical deprivation cycles, also showed only partial compensation. Nevertheless, the rate of tissue recovery may differ from that of whole-body growth (Nicieza and Metcalfe 1997; Metcalfe et al. 2002). Thus, when feeding resumed, prefasted fish regained liver size and main tissue components, as reported for other species (Blasco et al. 1992; Navarro et al. 1992). Excessive accumulation of lipids may lead to steatosis (Kalogeropoulos et al. 1992; Spisni et al. 1998), and hepatic metabolism is compromised at low temperatures (Gallardo et al. 2003). However, the mobilisation observed during the recovery of the cold group indicates that this situation may be reversed. The cold group did not show compensation dynamics in growth, which might explain why the unproductive period in gilthead sea bream farms sometimes extends into spring (Tort et al. 1998). In contrast to cold exposure, thermal fluctuations minimized hepatic alterations and the changes in main components as a result of the short refeeding episodes. Therefore the recovery of the fluctuating group would entail lower energy expenditure in tissue repair, and so the growth rate would be recovered earlier than in the cold group.

Some results may contribute to improving the culture and management of gilthead sea bream. First, when fish are subjected to stress, especially cold shifts, hepatic lipid metabolism may be altered by excessive fat depots. Second, the great plasticity of the liver glycogen store indicates that the use of carbohydrates as fuel in this species needs to be reconsidered. Current high-energy, fat-enriched diets favour fish fattiness and are unsuitable, even harmful, for this species. Third, the feeding strategy throughout the cold season should take into account the occurrence of occasional short warm periods, supplying an adequate diet and ration only when water temperature rises above 12 °C.

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References

Ali, M., Nicieza, A., and Wootton, R.J. 2003. Compensatory growth in fishes: a response to growth depression. Fish Fish. **4**: 147–190.

Allain, C.C., Poon, L.S., Chan, C.S.G., Richmond, W., and Fu, P.C. 1974. Enzymatic determination of total serum cholesterol. Clin. Chem. **20**: 470–475.

Bastrop, R., Spangenberg, R., and Jürss, K. 1991. Biochemical adaptations of juvenile carp (*Cyprinus carpio* L.) to food deprivation. Comp. Biochem. Physiol. A, **98**: 143–149.

Beamish, F.W.H. 1964. Influence of starvation on standard and routine oxygen consumption. Trans. Am. Fish. Soc. **93**: 103–107.

Blasco, J., Fernández, J., and Gutiérrez, J. 1992. Fasting and refeeding in carp, *Cyprinus carpio* L.: the mobilisation of reserves and plasma metabolite and hormone variations. J. Comp. Physiol. B, **162**: 539–546.

Christie, W.W. 1982. Lipids analysis. 2nd. ed. Pergamon Press, Oxford, UK.

Collins, A.L., and Anderson, T.A. 1995. The regulation of endogenous energy stores during starvation and re-feeding in the somatic tissues of the golden perch. J. Fish Biol. **47**: 1004–1015.

Dey, I., Csaba, B., Wiik, T., Halver, J.E., and Farkas, T. 1993. Molecular and structural composition of phospholipid membranes in livers of marine and freshwater fish in relation of temperature. Proc. Natl. Acad. Sci. U.S.A. **90**: 7498–7502.

Du Preez, H.H., Strydon, W., and Winter, P.E.D. 1986. Oxygen consumption of two marine teleosts *Lithognathus mormyrus* (Linnaeus, 1758) and *Lithognathus lithognathus* (Cuvier 1830) (Teleostei: Sparidae). Comp. Biochem. Physiol. A, **85**: 313–381.

Egginton, S., and Sidell, B.D. 1989. Thermal acclimation induces adaptive changes in subcellular structure of fish skeletal muscle. Am. J. Physiol. **256**: R1–R9.

Eroldogan, O.T., Kumlu, M., Kiris, G.A., and Sezer, B. 2006. Compensatory growth response of *Sparus aurata* following different starvation and refeeding protocols. Aquac. Nutr. **12**: 203–210.

Folch, J., Lees, M., and Stanley, G.H.S. 1957. A simple method for the isolation and purification of total lipids from animal tissues. J. Biol. Chem. **226**: 497–509.

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Foster G.D., and Moon, T.W. 1991. Hypometabolism with fasting in yellow perch (*Perca flavescens*): a study of enzymes, hepatocyte metabolism, and tissue size. Physiol. Zool. **64**: 259–275.

Fraga, F. 1956. Determinación del glucógeno en moluscos con el reactivo de antrona. Invest. Pesq. **3**: 69.

Gallardo, M.A., Sala-Rabanal, M., Ibarz, A., Padrós, F., Blasco, J., Fernández, J., and Sánchez, J. 2003. Functional alterations associated with the 'winter syndrome' in gilthead sea bream (*Sparus aurata*). Aquaculture, **223**: 15–27.

Grigorakis, K., and Alexis, M.N. 2005. Effects of fasting on the meat quality and fat deposition of commercial-size farmed gilthead sea bream (*Sparus aurata*, L.) fed different dietary regimes. Aquac. Nutr. **11**: 341–344.

Guderley, H. 2004. Locomotor performance and muscle metabolic capacities: impact of temperature and energetic status. Comp. Biochem. Physiol. B, **139**: 371–382.

Guderley, H., Lapointe, D., Bédard, M., and Dutil, J.D. 2003. Metabolic priorities during starvation: enzyme sparing in liver and white muscle of Atlantic cod, *Gadus morhua* L. Comp. Biochem. Physiol. A, **135**: 347–356.

Hazel, J.R. 1984. Effects of temperature on the structure and metabolism of cell membranes in fish. Am. J. Physiol. **246**: 460–470.

Ibarz, A., Fernández-Borràs, J., Blasco, J., Gallardo, M.A., and Sánchez, J. 2003. Oxygen consumption and feeding rates of gilthead sea bream (*Sparus aurata*) reveal lack of acclimation to cold. Fish Physiol. Biochem. **29**: 313–321.

Ibarz, A., Blasco, J., Beltrán, M., Gallardo, M.A., Sánchez, J., Sala, R., and Fernández-Borràs, J. 2005. Cold-induced alterations on proximate composition and fatty acid profiles of several tissues in gilthead sea bream (*Sparus aurata*). Aquaculture, **249**: 477–486.

Ibarz, A., Beltrán, M., Fernández-Borràs, J., Gallardo, M.A., Sánchez, J., and Blasco, J. 2007. Alterations in lipid metabolism and use of energy depots of gilthead sea bream (*Sparus aurata*) at low temperatures. Aquaculture, **262**: 470–480.

Itaya, K., and Ui, M. 1965. Colorimetric determination of free fatty acids in biological fluids. J. Lipid Res. **6**: 16–20.

Juaneda, P., and Rocquelin, G. 1985. Rapid and convenient separation of phospholipids in rat heart using silica cartridges. Lipids, **20**: 40–41.

Kalogeropoulos, N., Alexis, M.N., and Henderson, R.J. 1992. Effects of dietary soybean and cod-liver oil levels on growth and body composition of gilthead seabream (*Sparus aurata*). Aquaculture, **104**: 293–308.

Lemarié, G., Gasset, E., Cam, D., and De-La Fonchais, E. 1992. Models of oxygen consumption for sea bass (*Dicentrarchus labrax*) and sea bream (*Sparus aurata*). Ichtyophysiol. Acta, **15**: 55–68.

McGowan, M.W., Artiss, J.D., Strandbergh, D.R., and Zak, B. 1983. A peroxidase-coupled method for the colorimetric determination of serum triglycerides. Clin. Chem. **29**: 538–542.

Metcalfe, N.B., Bull, C.D., and Mangel, M. 2002. Seasonal variation in catch-up growth reveals state-dependent somatic allocations in salmon. Evol. Ecol. Res. **4**: 871–881.

Metón, I., Fernández, F., and Baanante, I.V. 2003. Short- and long-term effects of refeeding on key enzyme activities in glycolysis–gluconeogenesis in the liver of gilthead seabream (*Sparus aurata*). Aquaculture, **225**: 99–107.

Navarro, I., Gutiérrez, J., and Planas, J. 1992. Changes in plasma glucagon, insulin and tissue metabolites associated with prolonged fasting in rainbow trout (*Salmo trutta fario*) during two different seasons of the year. Comp. Biochem. Physiol. A, **102**: 401–407.

Nicieza, A.G., and Metcalfe, N.B. 1997. Growth compensatory in juvenile Atlantic salmon: responses to depressed temperature and food availability. Ecology, **78**: 2385–2400.

Padrós, F., Tort, L., and Crespo, S. 1996. Winter disease in the gilthead seabream *Sparus aurata*: some evidence of a multifactorial etiology. *In* Seabass and seabream culture: problems and prospects: handbook of contributions and short communications presented at the International Workshop on Seabass and Seabream Culture: Problems and Prospects, Verona, Italy, 16–18 October 1996. *Edited by* B. Chatain, M. Saroglia, J. Sweetman, and P. Lavens. European Aquaculture Society, Oostende, Belgium. pp. 305–307.

Power, D.M., Melo, J., and Santos, C.R. 2001. The effect of food deprivation and refeeding on the liver, thyroid hormones and transthyretin in sea bream. J. Fish Biol. **56**: 374–387.

Prosser, C.L. 1991. Environmental and metabolic animal physiology. Wiley-Liss, New York.

Riemenschneider, W.K., and Sidell, B.D. 2002. Cold acclimation induces proliferation of sarcoplasmatic reticulum without increase in Ca^{2+}-ATPase activity in white axial muscle of striped bass (*Morone saxatilis*). J. Exp. Zool. **292**: 231–240.

Sala-Rabanal, M., Sánchez, J., Ibarz, A., Fernández-Borràs, J., Blasco, J., and Gallardo, M.A. 2003. Effects of low temperatures and fasting on hematology and plasma composition of gilthead sea bream (*Sparus aurata*). Fish Physiol. Biochem. **29**: 105–115.

Sarusic, G. 1999. Clinical signs of the winter disease phenomenon in sea bream (*Sparus aurata*, L.). Bull. Eur. Assoc. Fish Pathol. **19**(3): 113.

Sheridan, M.A. 1988. Lipid dynamics in fish: aspects of absorption, transportation, deposition and mobilization. Comp. Biochem. Physiol. B, **90**(4): 679–690.

Sheridan, M.A., and Mommsen, T.P. 1991. Effects of nutritional state on *in vivo* lipid and carbohydrate metabolism of coho salmon, *Oncorhynchus kisutch*. Gen. Comp. Endocrinol. **81**: 473–483.

Spisni, E., Tugnoli, M., Ponticelli, A., Mordeni, T., and Tomasi, V. 1998. Hepatic steatosis in artificially marine teleosts. J. Fish Dis. **21**: 177–184.

Tocher, D.R., and Harvie, D.G. 1988. Fatty acid composition of the major phosphoglycerides from fish neural tissues: (*n*-3) and (*n*-6) polyunsaturated fatty acids in rainbow trout (*Salmo gairdneri*) and cod (*Gadus morhua*) brains and retinas. Fish Physiol. Biochem. **5**: 229–239.

Tort, L., Padrós, F., Rotllant, J., and Crespo, S. 1998. Winter syndrome in the gilthead sea bream *Sparus aurata*. Immunological and histopathological features. Fish Shellfish Immunol. **8**: 37–47.

Tort, L., Hernández, A., Ibarz, A., Gallardo, M.A., Blasco, J., Padrós, J., and Fernández, J. 2005. Winter syndrome in sea bream (*Sparus aurata*). *In* Society for Experimental Biology, Annual Main Meeting, Barcelona. Comp. Biochem. Physiol. A, **141**: S330.

van Dijk, P.L.M., Hardewig, I., and Holker, F. 2005. Energy reserves during food deprivation and compensatory growth in juvenile roach: the importance of season and temperature. J. Fish Biol. **66**(1): 167–181.

Venou, B., Alexis, M.N., Fountoulaki, E., Nengas, I., Apostolopoulou, M., and Castritsi-Cathariou, I. 2003. Effect of extrusion of wheat and corn on gilthead sea bream (*Sparus aurata*) growth, nutrient utilization efficiency, rates of gastric evacuation and digestive enzyme activities. Aquaculture, **25**: 207–223.

Wallaert, C., and Babin, P.J. 1994. Effects of temperature variations on dietary lipid absorption and plasma lipoprotein concentrations in trout (*Oncorhynchus mykiss*). Comp. Biochem. Physiol. B, **109**: 473–487.

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